COMMUNITY ASSEMBLY OF XERIC-ADAPTED ANURANS AT MULTIPLE SPATIAL SCALES

A Dissertation

by

GAGE HART DAYTON

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2005

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Lee A. Fitzgerald
Committee Members,	James R. Dixon
	Thomas E. Lacher, Jr.
	Xinyuan Ben Wu
Head of Department,	Robert Brown

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ABSTRACT

Community Assembly of Xeric-adapted Anurans at Multiple Spatial Scales. (December 2005)

Gage Hart Dayton, B.S., Humboldt State University;

M.S., Texas A&M University

Chair of Advisory Committee: Dr. Lee A. Fitzgerald

The distribution and abundance of organisms is influenced by historical, abiotic, and biotic factors. The goal of my dissertation was to determine the distribution of anurans in the Big Bend region of the Chihuahuan Desert and to examine how abiotic and biotic factors shape the composition and structure of anuran communities at multiple spatial scales. My approach relied on extensive field surveys, laboratory and field experiments, and GIS modeling.

Results from field surveys and reciprocal transplant studies of tadpoles indicate that abiotic conditions of the breeding site most likely do not play a significant role in causing the segregation of species among individual breeding pools. I used laboratory and mesocosm experiments to test for indirect and direct effects of predators on growth and survival of *S. couchii* tadpoles. I found that *S. couchii* tadpoles do not alter their behavior in the presence of predators and are very susceptible to predation. Although tadpoles reared with predators suffered high mortality rates, they metamorphosed significantly faster than tadpoles reared without predators. The reduced time to

metamorphose is likely a result of the thinning of intraspecific competitors. Because the primary cause of death for *S. couchii* tadpoles is desiccation due to pond drying, predators may play an important role in facilitating metamorphosis by decreasing competitors and thus increasing per capita resources, therefore decreasing time to metamorphosis for the surviving tadpoles.

At the landscape level anuran distributions seem to be influenced by environmental factors that influence the survival of the adult stage. At the level of the breeding site, microhabitat and abiotic components of the aquatic environment do not seem to play an important role in influencing breeding site use by different species. Rather, it seems likely that predation on tadpoles by predators is important in limiting the distribution of some species and that the fast-developing *S. couchii* may exclude other species from using sites via oophagy and predation on small tadpoles. My research elucidates the fact that in order to understand factors important in regulating ecological communities it is important to examine both abiotic and biotic factors at multiple spatial scales.

DEDICATION

I would like to dedicate my dissertation to my entire family. Thanks for your love and support. You are the most important part of my life. In memory of Gogo, I miss you.

ACKNOWLEDGEMENTS

My deepest thanks go out to my advisory committee: Drs. Lee A. Fitzgerald, James R. Dixon, Xinyuan B. Wu, and Thomas E. Lacher, Jr. Each of you had very different but important roles in helping me formulate my ideas and guide me throughout my studies. I am grateful for your advice, mentoring, discussions, and friendship. Thanks.

Although I conducted this research it is truly a collaborative effort from discussions to field assistance to experimental design and manuscript preparation. This work would not have been possible without the tremendous support of the staff at Big Bend National Park. R. Skiles and V. Davila provided essential logistic assistance and administrative support. R. Jung, S. Droege, and S. Walls all had a big hand in helping to make the Big Bend amphibian research continue for 7 years. Field assistance was provided by K. Bonine, S. Claeson, E. Dayton, P. Dayton, A. De la Reza, J.E. Wallace, S. Raimondo, M. Rosenshield, S. Williamson, L. Fitzgerald, P. Lavin, J.R. Dixon. This work was supported in part by funding from the National Park Service and the Environmental Protection Agency through the PRIMENet (Park Research and Intensive Monitoring of Ecosystems Network) program, the U.S. Geological Survey's ARMI (Amphibian Research and Monitoring Initiative), Tom Slick Graduate Fellowship, Francis Bacon Memorial Fund, Society of Wetlands Scientists student research grant, and the Texas Water Resource Initiative Mills Scholarship.

I especially thank those who helped facilitate my survey work in Mexico: Cañon de Santa Elena Protected Area, Del Carmen Protected Area, and CEMEX biologists, Pablo Dominguez, Julio Carrera, Vidal Davila, Jim Dixon, Lee Fitzgerald, Alberto Garza, David Garza, Pablo Lavin, Bonnie McKinney, Bill McKinney, Howard Ness, Ramón Olivas, and Raymond Skiles provided logistical, field, and anecdotal support. Funding for this portion of my research was provided by the National Park Service Intermountain Region International Conservation, Amphibian Research and Monitoring Initiative, Park Research and Intensive Monitoring of Ecosystems Network, and the Tom Slick Graduate Fellowship. I was assisted by several people in the field including: Ana Gatica and Ricardo Núñez, Gilberto Herrera, Oscar Hinojosa y Verónica Sosa. I am indebted to the following Universities, Museums, and Natural History Collections for providing me with historical data on specimen collections in one or more of the three protected areas: Cornell University, University of Michigan's Museum of Zoology, Museum of Southwestern Biology, Illinois Natural History Survey, Museum of Vertebrate Zoology at the University of California, Texas Cooperative Wildlife Collections, Monte L. Bean Life Science Museum, Museum of Texas Tech University, Museum of Natural Science at Louisiana State University, Tulane Museum of Natural History, Unites States Natural History Museum at the Smithsonian Institution, Strecker Museum, Natural History Museum at the University of Kansas, Florida Museum of Natural History, The American Museum of Natural History, The Field Museum of Natural History, Carnegie Museum of Natural History, Museum of Comparative Biology at Harvard, California Academy of Sciences, The Academy of Natural Sciences, Texas

Memorial Museum, Centennial Museum, Florida Museum of Natural History, Colorado University Museum, Peabody Museum of Natural History, Cincinnati Museum Center, Georgia Museum of Natural History, Sam Noble Okalahoma Museum of Natural History, San Diego Natural History Museum, Arizona State University Natural History Museum, Sul Ross State University Natural History Museum. All work followed the guidelines of the permits issued to me by the National Park and the Secretaria del Medio Ambiente, Recursos Naturales Y Pesca, I thank these institutions for allowing me to conduct my research in these protected habitats.

Finally, I would like to thank my family Paul, Linnea, Anaika, Savanna, Camille and Lily for all their support and love. I would especially like to thank Lily for her support at home, in the field, and many many edits. I couldn't have done it without you guys.

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CHAPTER I

INTRODUCTION

The local distributions of many amphibians are limited by constraints on aquatic larval stages (Skelly 1997, Skelly et al. 1999). Amphibian larval ecology can be generalized as a gradient, with species well-suited to coexist with predators occurring in permanent water and species that are active and competitive occurring in ephemeral pools. Abiotic factors such as hydroperiod, and biotic factors such as species interactions, thus work in a complex system of trade-offs that influences the ability of species' larvae to successfully reach metamorphosis. Interactions between abiotic and biotic factors greatly determine the distribution and persistence of anuran species. Hydroperiod, interspecific competition, and predation of larval amphibians are processes that influence distributions and persistence of amphibian species (Woodward 1982b, 1983, Skelly 1995, McDiarmid and Altig 1999). The majority of what we know today regarding mechanisms that structure amphibian communities comes from studies conducted in eastern United States (Wilbur 1982, Morin et al. 1983, Wilbur and Fauth 1990, Gascon 1991, Werner 1992, Gascon 1993, Skelly 1994, Werner and McPeek 1994, Gascon 1995, Skelly 1995, 1996, Werner and Anholt 1996, Skelly 2001) and tropical forests of Central and South America (Heyer et al. 1975, Gascon 1991, 1992, 1993, 1995).

This dissertation follows the style of Ecology.

High rainfall over large areas in these regions creates a heterogeneous environment of pools that persist for several months. The relatively long hydroperiods of pools in mesic environments allows amphibians with larvae of variable developmental periods to successfully reproduce. Moist conditions and extensive forest cover provide suitable habitat for movement of adults between pools, and the extended breeding period enables asynchronous breeding of species. Hence, in mesic environments anuran assemblages are relatively species-rich with predictable phenology attributed to the breeding biology of component species. Large breeding sites with long hydroperiods also result in an increase of both aquatic and terrestrial predators that are important in structuring amphibian communities in these regions (Wellborn et al. 1996). Characteristics of these temperate and tropical environments provide a relatively stable and predictable, but perhaps more complex, habitat that supports greater amphibian species richness compared to desert regions.

In contrast to temperate and tropical regions, deserts are characterized by patchy vegetation, higher temperatures, and highly variable, seasonal, precipitation that varies in location, intensity, and frequency on a year to year basis (Whitford 2002). Individual breeding sites for desert-dwelling amphibians vary in size, depth, duration, and are not always present annually. Amphibians in these systems usually breed in a given pool only once a year and often do not breed on an annual basis due to unpredictability of seasonal rains (Woodward 1984). However, the presence of water and breeding adults does not necessarily result in increased fitness as the majority of pools that amphibians breed in dry up before tadpoles successfully metamorphose (Newman 1987). High

summer temperatures, monsoon rains, winter droughts, and patchy vegetation may inhibit movement of amphibians across desert landscapes. Desert amphibians spend the majority of the year in a dormant state, only coming to the surface to feed and breed during seasonal rains. Thus, compared to temperate and tropical regions where presence of water is much more predictable and conducive to successful reproduction, amphibians in desert regions face a harsher set of conditions and most likely go several years between successful breeding events. The harsh desert environment (for both amphibians and researchers) combined with sporadic rain events has led researchers to regard desert amphibian communities as relatively simplistic compared to temperate and tropical amphibian communities (Woodward and Mitchell 1991). Not surprisingly, there is a paucity of research examining distribution patterns of anurans in desert regions throughout the world (Woodward and Mitchell 1991) and the majority of this research has focused purely on distributions and habitat associations of adults. However, recent research examining patterns of breeding site use in four desert anurans in the Chihuahuan desert revealed that their distributions were in fact non-random, and co-occurrence of species in temporary pools was significantly less than would be expected if they used the environment in a random fashion (Dayton and Fitzgerald 2001). Furthermore, results from laboratory experiments suggested competition and predation were important mechanisms affecting species persistence and distribution patterns of anurans that breed in temporary desert pools.

The paucity of research that has focused on xeric-adapted amphibians is alarming, considering the fact that deserts make up approximately 33% of the terrestrial

environment (Whitford 2002) and that some of the most vulnerable amphibians in North America are found in arid regions (Bradford personal communication). The objectives of my dissertation research were to determine the distribution of anurans in the Big Bend Region of the Chihuahuan Desert and to examine abiotic and biotic factors that influence the distribution of anurans at multiple spatial scales across a xeric environment. The five main objectives of my dissertation are:

1) Create a current inventory of the amphibian species in three protected areas in the Big Bend region of the Chihuahuan Desert: Big Bend National Park, U.S.A., Maderas del Carmen Protected Area, Mexico, and Cañon de Santa Elena Protected Area, Mexico.
2) Examine the importance of priority effects as a potential factor that limits amphibian distribution at specific breeding sites.
3) Create and test landscape-level habitat suitability models for a guild of anurans that breed in ephemeral pools.
4) Examine differences in microhabitat characteristics associated with breeding sites of a guild of ephemeral pool-breeding anurans.
5) Examine the role that aquatic predators play in influencing growth, development, survivorship, and distribution of *Scaphiopus couchii*.

Study System

My study was conducted in the Big Bend Region of the Chihuahua Desert. The majority of my field research was conducted within Big Bend National Park, Texas.

Mesocosm studies were conducted at Elephant Mountain Wildlife Management Area, Texas. Several sampling trips were made to two protected areas in Mexico: Maderas del Carmen Protected Area and Cañon de Santa Elena Protected Area. Data collection for my study began in June 1998 and continued through August 2005. Elevation throughout my study area ranges from 600 m along the Rio Grande to approximately 3000 m in the Maderas del Carmen Mountains. Mean summer and winter daytime temperatures in Big Bend National Park range from 37^{o}C and 18^{o} C, respectively, with extremes of 46^{o}C in the summer and -4^{o}C in the winter. Mean annual precipitation is 38 cm with 75% of the rain occurring in intense isolated thunderstorms from May to September.

Dissertation Format

Each chapter of this dissertation represents a set of specific research findings written in the form of a scientific paper: overview, introduction, methods section, discussion, and acknowledgements. Chapter I presents a general overview of factors that regulate assemblages of anurans across the landscape. Chapter II provides a current representation of the distribution patterns of anurans in the Big Bend Region, resulting from several years of field survey work in Big Bend National Park, U.S.A, Maderas del Carmen Protected Area, Mexico, and Cañon de Santa Elena Protected Area, Mexico. Chapter III covers the development and testing of habitat suitability models for four anuran species that breed in temporary desert pools. In chapter IV, I report and discuss results from field observations and laboratory studies that suggest oophagy may be an important factor limiting the local distribution of desert anurans. Chapter V examines

the role of intraspecific competition and predation on tadpole metamorphosis and survivorship. Chapter VI examines whether characteristics of breeding site are important in limiting species occurrence. In this chapter I used reciprocal transplants to compare survivorship of tadpoles reared in temporary pools, where they occur naturally, to survivorship of tadpoles in pools where they are not known to occur. I also examine habitat characteristics of breeding sites and test for differences among sites occupied by different species. Chapter VII summarizes my overall findings and conclusions.

CHAPTER II

BASELINE INVENTORY OF AMPHIBIANS IN THE MADERAS DEL CARMEN AND CAÑON DE SANTA ELENA PROTECTED AREAS, MEXICO, AND BIG BEND NATIONAL PARK, TEXAS, USA

Overview

I conducted surveys for amphibians in Big Bend National Park, Texas, Cañon de Santa Elena Protected Area, Mexico, and the Maderas del Carmen Protected Area, Mexico. In Big Bend National Park I found Red-spotted Toads (*Bufo punctatus*), Western Green Toads (*B. debilis*), Texas Toads (*B. speciosus*), Narrow-mouthed Toads (*Gastrophryne olivacea*), Couch's Spadefoots (*Scaphiopus couchii*), Rio Grande Leopard Frogs (*Rana berlandieri*), Bullfrogs (*Rana catesbeiana*), Canyon Treefrogs (*Hyla arenicolor*), and Spotted Chirping Frogs (*Syrrhophus guttilatus*). In Cañon de Santa Elena Protected Area I found *B. debilis, B. punctatus, B. speciosus, G. olivacea, S. couchii, R. berlandieri, R. catesbeiana, S. guttilatus* and *H. arenicolor*. In the Maderas del Carmen Protected Area I found *B. punctatus, B. debilis, B. speciosus, G. olivacea, S. couchii, R. berlandieri,* and *H. arenicolor.*

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Introduction

In the United States, the National Park Service was established in 1916 to protect and preserve natural areas. Yet in 1995 biotic inventories in approximately 80% of the National Parks remained < 80% complete, with many taxon groups receiving very little

attention (Stohlgren et al. 1995). Stohlgren et al. (1995) found that high-profile organisms such as birds, mammals, and vascular plants have been more thoroughly surveyed than other taxonomic groups such as invertebrates, fungi, and amphibians. Approximately 55% of the 252 parks surveyed by Stohlgren et al. (1995) reported the inventory of amphibians was "poor to none." The paucity of baseline inventory data for amphibians is especially alarming considering the global decline in amphibian populations that has taken place over the past 30 years (Stuart et al. 2004). This lack of baseline data on flora and fauna in protected areas is a common problem throughout the world and is a major hindrance to the development of conservation and management strategies (Oldfield and Sheppard 1997, Yahnke et al. 1998, Schneider and Burnett 2000, Ervin 2003).

The Big Bend Region of the Chihuahuan Desert represents a relatively unique situation in that there are three separate yet adjoining protected areas that form a single land mass of protected habitats. Situated on both sides of the Rio Grande River, Big Bend National Park, USA, Cañon de Santa Elena Protected Area, MX, and the Maderas del Carmen Protected Area, MX are critical components of the Chihuahuan Desert Ecoregion and Madrean pine-oak woodlands ecosystem (Fig. 1). These regions have been identified as a biodiversity hotspot (Mittermeier et al. 2005) and a high biodiversity area Wilderness Area (Mittermeier et al. 2002).

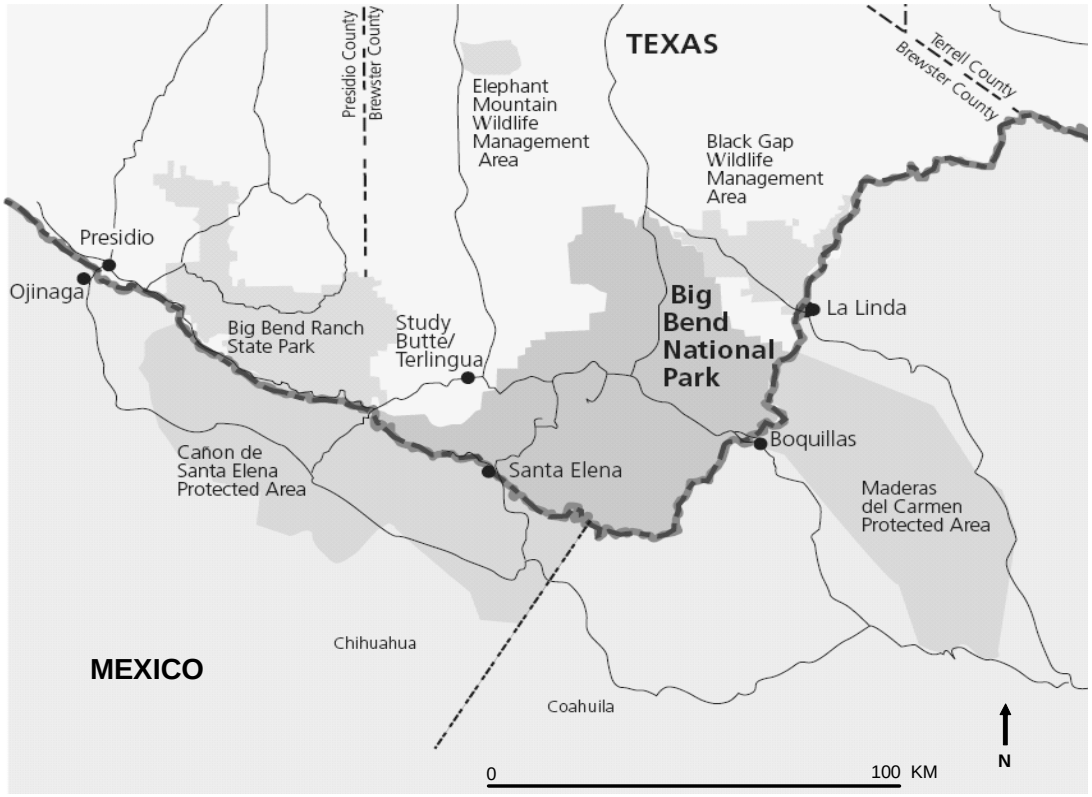

Figure 1. Regional map of Big Bend National Park, Cañon de Santa Elena Protected Area, and Maderas del Carmen Protected Area.

The three protected areas all contain desert lowland habitat as well as montane forests. The Maderas del Carmen Protected Area and Cañon de Santa Elena Protected Area have several habitats that are unique from Big Bend such as perennial streams in the higher elevations, extensive pine and fir forests, and large desert grasslands (Taylor et al. 1946). Big Bend National Park was established in 1944 and protects over 323,760 hectares of Chihuahuan Desert. The Cañon de Santa Elena and Maderas del Carmen Protected Areas were established in 1994 to protect more than 485,640 hectares.

Throughout the past century, there have been numerous scientific studies conducted on amphibians within BBNP, however, only a few of these studies focused on assembling species lists (Strecker 1909, Schmidt and Smith 1944, Minton 1959). Indeed, there has not been an inventory of amphibians in Big Bend National Park since Minton's work in 1959. And although several cursory surveys for amphibians in portions of the Mexican Protected Areas have been conducted over the past century (Gloyd and Smith 1942, Schmidt and Owens 1944, Taylor et al. 1946), these surveys were not complete and only covered a small area. The results of these studies, as well as other published information, provide a cursory overview of the amphibian communities in the three protected regions (Table 1).

As part of a joint effort with park and protected area staff from the three protected areas, I conducted field surveys for amphibians. The objectives of this study were to survey for amphibians in a wide variety of habitats within the three protected

Table 1. Historical distributions of amphibian species in Cañon de Santa Elena Protected Area, Maderas del Carmen Protected Area, and Big Bend National Park. Inclusion is based on range maps with locality data in one of the three Parks/Protected Areas (verified through literature and/or museum records).

Species	Maderas del Carmen	Cañon de Santa Elena	Big Bend National Park
Acris crepitans	Morafka, 1977	Schmidt and Owens 1944	
Bufo debilis			Dayton et al. 2004
Bufo punctatus			Dayton and Fitzgerald 2001
Bufo speciosus	Morafka, 1977; Schmidt and Owens 1944		Dayton and Fitzgerald 2001
Bufo valliceps	Morafka, 1977; Schmidt and Owens 1944		
Bufo woodhousii	Minton 1959		Historical records exist
Gastrophryne olivacea			Dayton 2000
Hyla arenicolor	Morafka, 1977		Jung et al. 2002b
Rana berlandieri	Schmidt and Owens 1944		Jung et al. 2002a
Rana catesbeiana			Jung et al. 2002a
Scaphiopus couchii	Schmidt and Owens 1944		Dayton and Fitzgerald 2001
Spea multiplicata		Morafka 1977	Historical records exist
Syrrhophus guttilatus			Jung et al. 2002a

areas and create voucher collections of all the amphibian species detected. The ultimate goal was to establish a baseline survey of amphibians in this international region, with the intention that data collected during this period will serve as a reference point for future studies examining amphibians in this area. I present lists of species found in the areas, provide a discussion on the occurrence of each species, and compare the makeup of the amphibian assemblages among the three protected areas.

Methods

During the summers of 1998-2004, the U.S. Environmental Protection Agency, U.S. National Parks Service, U. S. Geological Survey, and Texas A&M University undertook an intensive joint project to create a baseline survey and ecological study of amphibians in Big Bend National Park. From 2002-2004, Texas A&M University, the National Park Service, and the Instituto Tecnologico de Ciudad Victoria conducted 5 separate surveys of amphibians in Cañon de Santa Elena Protected Area and Maderas del Carmen Protected Area and surrounding lands.

Sampling methods consisted of night driving, dip-net surveys, canoe surveys, and area-constrained searches (Dayton 2001, Dayton and Fitzgerald 2001, Jung et al. 2002a, Jung et al. 2002b, Dayton et al. 2004). For the majority of site selection, I relied upon Protected Area staff, private land owners, and the localities of recent rains. Voucher specimens (adults, tadpoles, and recently metamorphosed tadpoles) from Big Bend National Park, Cañon de Santa Elena Protected Area, and Maderas del Carmen

Protected Area were preserved and are housed at the Instituto Tecnologico de Ciudad Victoria and at the Texas Cooperative Wildlife Collections.

Results

Protected Area Summaries

Species richness in the three protected areas was relatively similar (Table 2). In the Maderas del Carmen Protected Area I sampled in low desert regions from Boquillas east to Pilares and at higher elevations in the Museo del Carmen. Lowland habitats included small springs, earthen tanks, and temporary pools. In the lower elevations I found *Bufo punctatus* Baird and Girard, 1852 (Red Spotted Toad), *Bufo speciosus* Girard, 1854 (Texas Toad), *Gastrophryne olivacea* Hallowell, 1857 (Plains Narrow-mouthed Toad), *Bufo debilis* Girard, 1854 (Green Toad), *Rana berlandieri* Baird, 1854 (Rio Grande Leopard Frog), and *Scaphiopus couchii* Baird, 1854 (Couch's Spadefoot Toad). Due to poor road conditions in the higher elevations within the Maderas del Carmen Protected Area, I was only able to survey sites in the Museo del Carmen and the surrounding foothill canyons. Habitats in the higher elevations consisted primarily of small running creeks, wet meadows, and man-made ponds. I collected two species, *Hyla arenicolor* Cope 1866 (Canyon Treefrog) and *R. berlandieri*, at higher elevation sites.

In Cañon de Santa Elena Protected Area the majority of the search effort focused on the lowland sites and along the Rio Grande.

Table 2. Presence absence data for each species in each of the three protected parks of Cañon de Santa Elena Protected Area, Maderas del Carmen, and Big Bend National Park.

Species	Maderas del Carmen	Cañon de Santa Elena	Big Bend National Park
Acris crepitans	absent	absent	absent
Bufo debilis	present	absent	present
Bufo punctatus	present	present	present
Bufo speciosus	absent	present	present
Bufo valliceps	absent	absent	absent
Bufo woodhousii	absent	absent	absent
Gastrophryne olivacea	present	present	present
Hyla arenicolor	present	present	present
Rana berlandieri	present	present	present
Rana catesbeiana	absent	present	present
Scaphiopus couchii	present	present	present
Spea multiplicata	absent	absent	absent
Syrrhophus guttilatus	absent	*present	present

*Several individuals heard calling from talus slopes at the eastern mouth of Santa Elena Canyon.

Low elevation habitats surveyed included creeks, tanks, and temporary water bodies along the road from Altares to Lajitas, as well as tanks and springs west of San Carlos. I also surveyed the banks of the Rio Grande from Paso Lajitas to the downstream entrance of Santa Elena Canyon. In the low elevation sites I found *B. punctatus*, *B. speciosus*, *G. olivacea*, *R. berlandieri,* and *S. couchii*. The only species detected in the higher elevations of the Sierra Ricas was *H. arenicolor*. This was a significant find in that, to the best of my knowledge, this record along with *H. arenicolor* detected in the foothills of the Sierra Rica at Las Pilas, are the first documented accounts of this species from the area. During the surveys along the Rio Grande I collected *R. berlandieri, B. speciosus, B. punctatus,* and *Rana catesbeiana* Shaw, 1802 (Bullfrog). I also heard *Syrrhophus guttilatus* Cope, 1879 (Spotted Chirping Frog) calling from the talus slopes at the downstream end of Santa Elena Canyon but was unable to collect any individuals.

In Big Bend National Park I conducted extensive surveys in lowland, upland, and river habitats. I found *B. punctatus* throughout the park in a wide variety of habitats but primarily associated with rocky regions and creek beds. *Bufo debilis* were found primarily in the northern regions of the park with a few isolated occurrences near Castolon. *Bufo speciosus* were found in northern regions of the park from Tornillo Flats throughout the North Rosillos, as well as at Rio Grande Village and Castolon. *Gastrophryne olivacea* were found throughout the park associated with a wide variety of habitats including rock pools, clay-lined stock tanks, and ephemeral pools in sandy clay loam soils. *Scaphiopus couchii* were found throughout the park associated primarily with sandy clay loam soils. *Hyla arenicolor* were found in the Chisos Mountains and

surrounding foothills. *Syrrhophus guttilatus* were detected in the Chisos, at Rio Grande Village, Santa Elena Canyon, Panther Creek, and at Burro Mesa Pouroff. *Rana berlandieri* were found at most permanent water bodies throughout the park. *Rana catesbeiana* were found along the Rio Grande and in the Beaver Pond at Rio Grande Village.

Species Summaries

Acris crepitans Baird, 1854 (Northern Cricket Frog). Brewster County, Texas is the western edge of *A. crepitans'* (Northern Cricket Frog) range in the Chihuahuan Desert (Conant and Collins 1998, Dixon 2000). There are published accounts of this species in Cañon de Santa Elena Protected Area and the Maderas del Carmen Protected Area, however, there are no records of *A. crepitans* in Big Bend National Park. *Acris crepitans* are associated with permanent and temporary water bodies in more temperate habitats to the north and east of the Big Bend region (Conant and Collins 1998). The most suitable habitat that I identified for this species during the surveys was a large lake northeast of Paso San Antonio in the Cañon de Santa Elena Protected Area. However, this man-made lake is in the middle of a very dry portion of the Chihuahuan desert surrounded by thick mesquite and creosote vegetation, and it is unlikely that *A. crepitans* could naturally colonize this area. No individuals were detected in the surveys and, other than the lake northeast of Paso San Antonio, and possibly the Beaver Pond at Rio Grande Village, I did not detect any habitat that I would characterize as suitable for this species. It should be noted that Morafka's (1977) maps indicate that *A. crepitans* exist

in Big Bend National Park; yet, to the best of my knowledge there has never been a voucher specimen of *A. crepitans* collected within the Park boundaries.

Bufo debilis (Fig. 2)—This species is relatively abundant where it occurs and tends to be associated with grasslands and soils that have relatively high clay content (Minton 1959, Dayton et al. 2004). In Big Bend National Park several *B. debilis* were collected in the northern region of the park from Tornillo Flats throughout the north Rosillos. A few individuals were also collected near Castolon. In the Maderas del Carmen Protected Area I found two individuals calling from a stock tank in mesquite scrub habitat in the flats to the southwest of Pilares. I did not find any *B. debilis* in Cañon de Santa Elena Protected Area, however, there was ample suitable habitat in the region of Paso Lajitas south to Manuel Benavides. Because of the seemingly suitable habitat found in Cañon de Santa Elena Protected Area, and the fact that *B. debilis* have been collected in close proximity to the Rio Grande River near the downstream entrance of Santa Elena Canyon in Big Bend National Park, I feel that it is likely that this species also occurs in Cañon de Santa Elena Protected Area with suitable habitat occurring in the clay loam flats between Paso Lajitas and San Carlos.

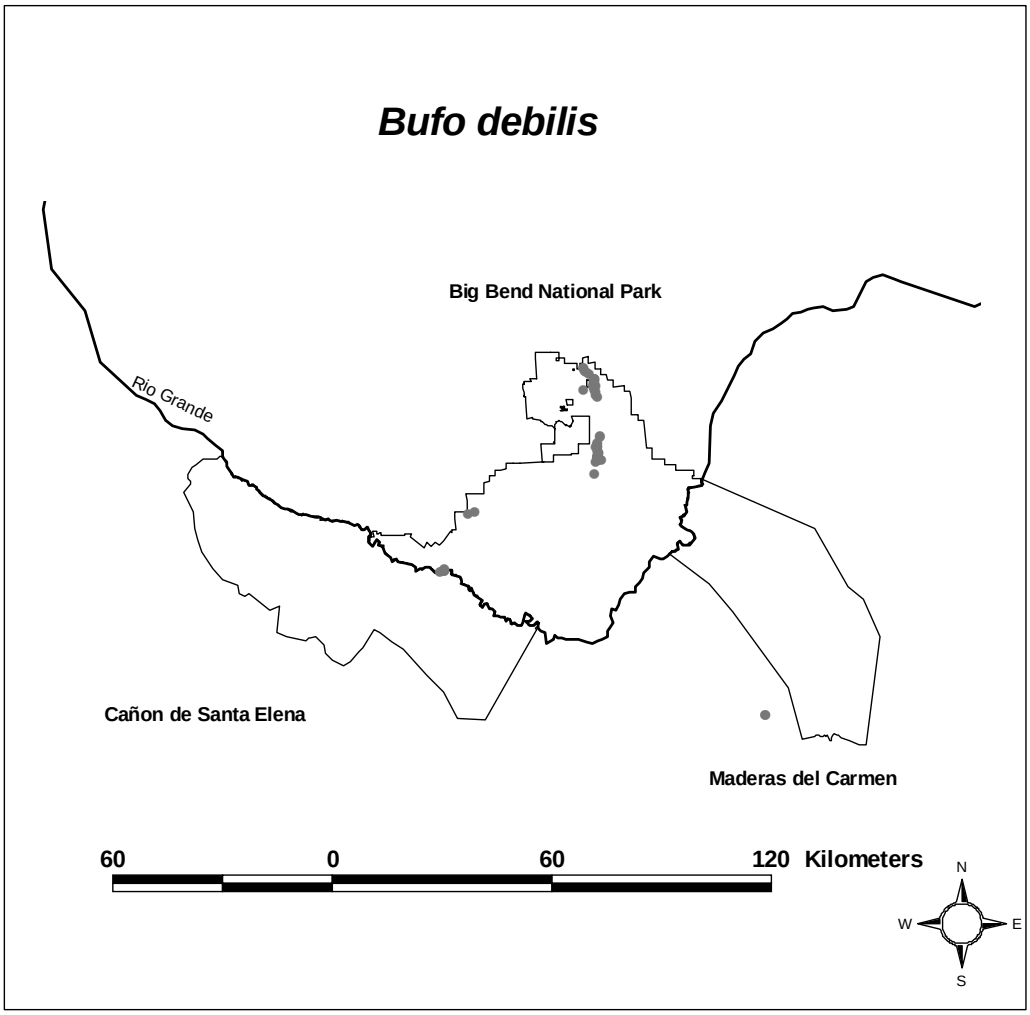

Figure 2. Localities of *B. debilis* in and near Big Bend National Park, Cañon de Santa Elena Protected Area, and the Maderas del Carmen Protected Area.

Bufo punctatus (Fig. 3)—I found this species to be widespread throughout Big Bend National Park, Cañon de Santa Elena Protected Area, and the Maderas del Carmen Protected Area. *Bufo punctatus* are commonly associated with temporary and permanent water bodies throughout their range (Conant and Collins 1998, Bradford et al. 2003). This species is considered to be more of a habitat generalist than many of the other species that inhabit this region (Dayton et al. 2004). I found *B. punctatus* in temporary pools, creek beds, stock tanks, permanent springs, and along the Rio Grande.

Bufo speciosus (Fig. 4)—In Big Bend National Park *B. speciosus* occur along the Rio Grande and in the North Rosillos and Dog Canyon regions (Jung et al. 2002a, Dayton et al. 2004). Although I did not find any *B. speciosus* in the Maderas del Carmen protected area, it is likely that they occur there due to the fact that I found them at Rio Grande Village and in close proximity to the northeastern boundary of the protected area along the road from Musquiz to Boquillas. Furthermore, there seems to be ample suitable habitat for *B. speciosus* in the Maderas del Carmen Protected Area in lowland areas where soils are dominated by clay loams. In Cañon de Santa Elena Protected Area I found *B. speciosus* along the Rio Grande, San Carlos Creek, throughout Altares Canyon, and at the large man-made lake northeast of Paso San Antonio. Previous studies in Big Bend National Park indicate that this species is relatively abundant where it occurs but that it is not a habitat generalist (Dayton et al. 2004). Rather, *B. speciosus* seem to be associated with clay loam soils and frequently inundated areas such as along the Rio Grande (Dayton et al. 2004).

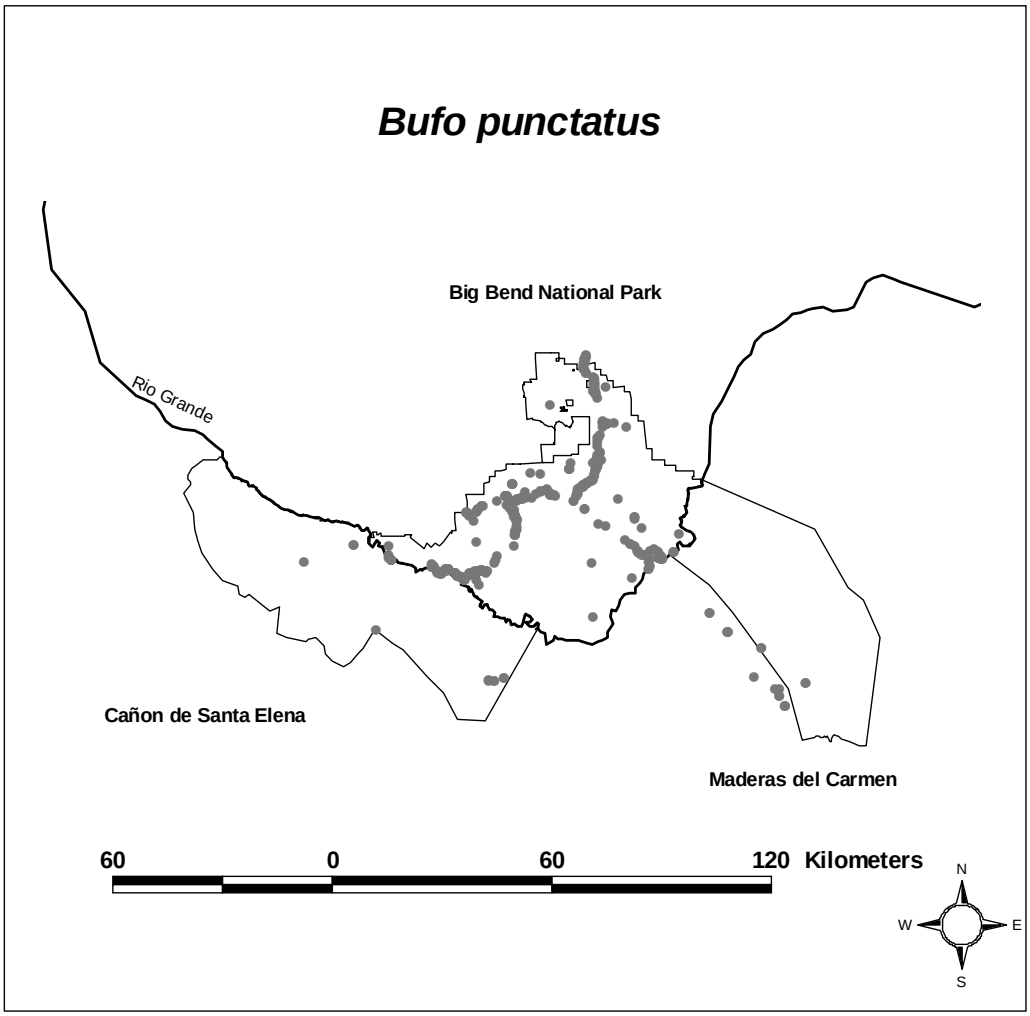

Figure 3. Localities of *B. punctatus* in and near Big Bend National Park, Cañon de Santa Elena Protected Area, and the Maderas del Carmen Protected Area.

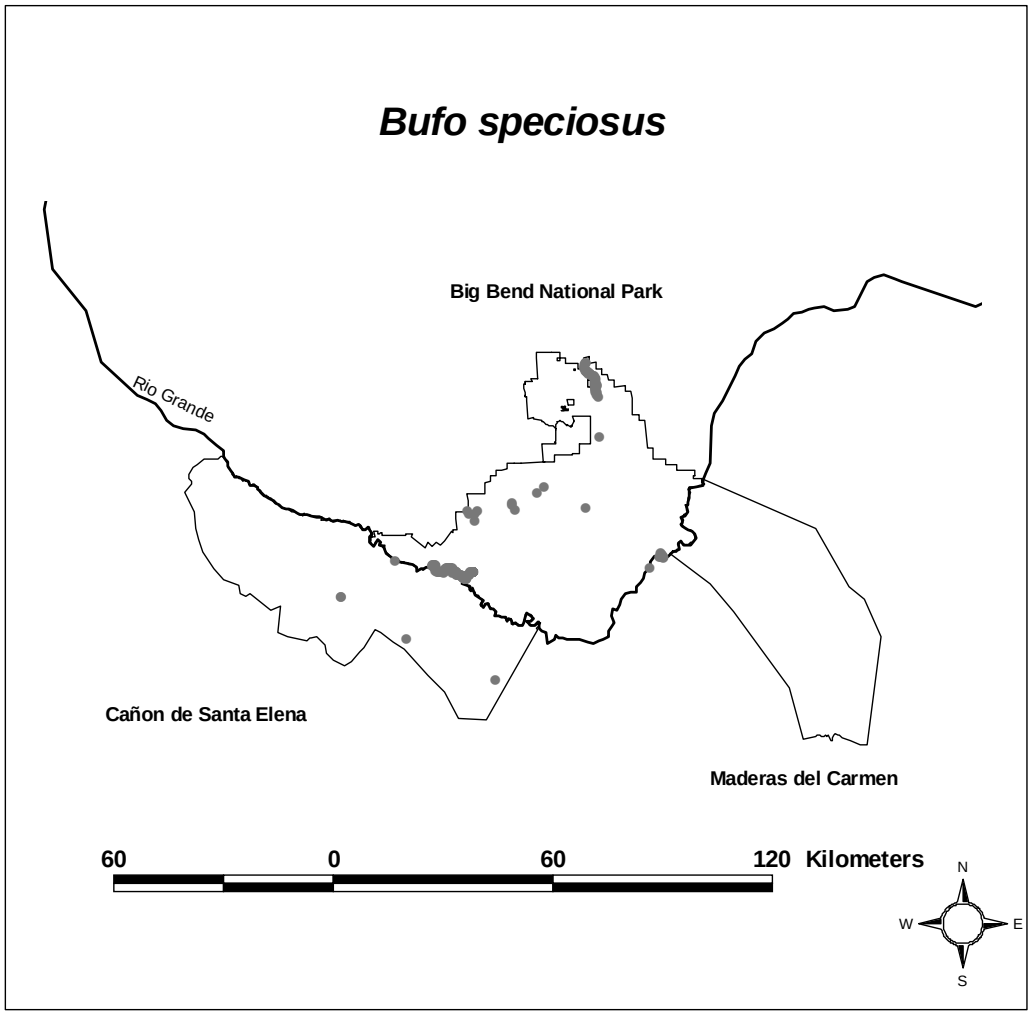

Figure 4. Localities of *B. speciosus* throughout Big Bend National Park, Cañon de Santa Elena Protected Area, and the Maderas del Carmen Protected Area.

Bufo valliceps Wiegmann, 1833 (Gulf Coast Toad)—Published accounts (Schmidt and Owens 1944, Morafka 1977) indicate that *B. valliceps* have been found in the Maderas del Carmen Protected Area and Cañon Santa Elena Protected Area, however, I did not detect any individuals in Big Bend National Park, Cañon de Santa Elena Protected Area, or the Maderas del Carmen Protected Area. The surveys, as well as results from searches of Natural History Collections, indicate that *B. valliceps* do not, and have not, occurred in Big Bend National Park during the past century. The Big Bend region is the western edge of the range for *B. valliceps* (Conant and Collins 1998) and if this species does occur in Big Bend National Park, Cañon de Santa Elena Protected Area, or the Maderas del Carmen Protected Area, it is most likely very rare.

Gastrophryne olivacea (Fig. 5) —I found *G. olivacea* in all three protected areas. This species has been reported to be rare throughout Big Bend National Park, however, my surveys indicate that *G. olivacea* are relatively common throughout Big Bend National Park and occur in a wide variety of habitats. Although I did not find a large number of individuals in either of the Mexican Protected Areas, this is probably due to the fact that they are very secretive and often difficult to detect (Sullivan et al. 1996, Dayton 2000) rather than an indication that they are rare.

Hyla arenicolor (Fig. 6)—I found *H. arenicolor* in all three of the protected areas. This species is believed to be a relict species in montane habitats in the Big Bend region, primarily confined to mountain tops and their surrounding foothills. In Big Bend National Park *H. arenicolor* were found in the Chisos Mountains and surrounding foothills. In Cañon de Santa Elena Protected Area I found *H. arenicolor* in the high

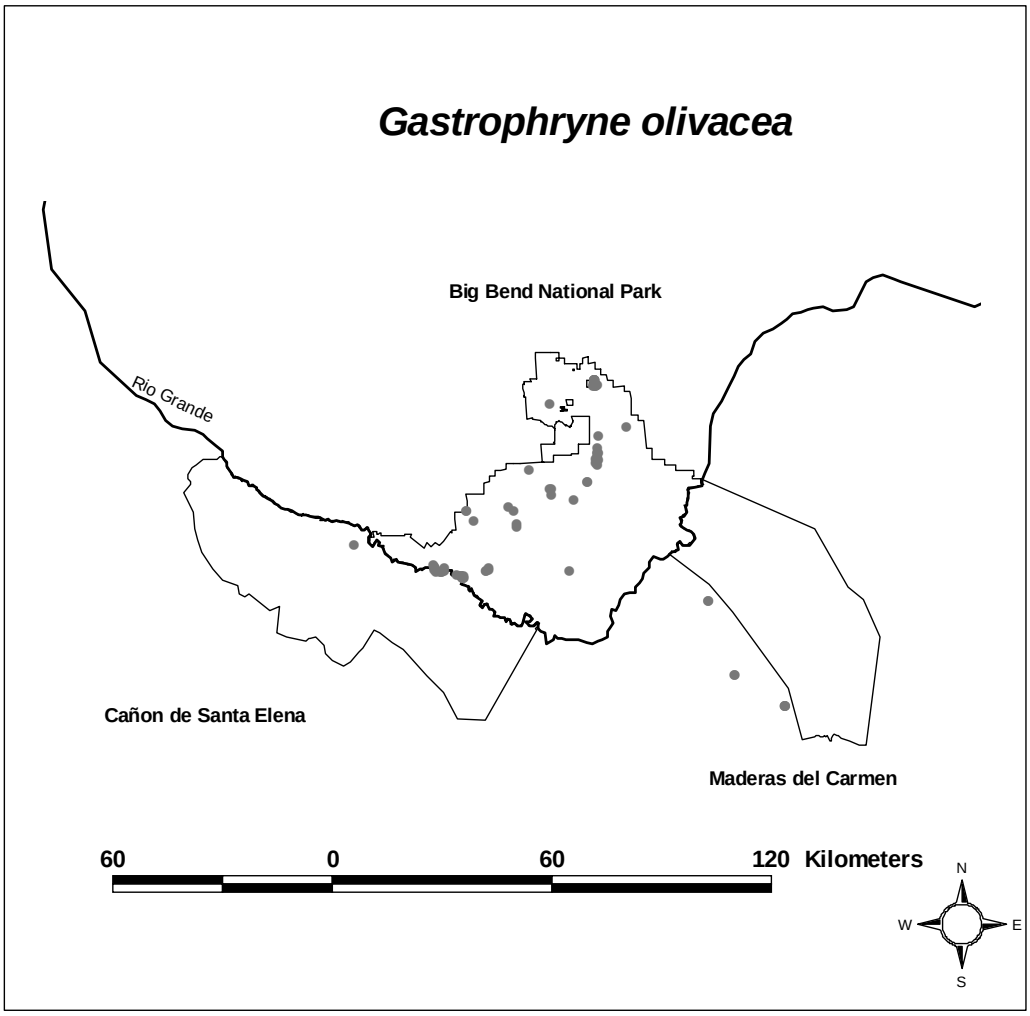

Figure 5. Localities of *G. olivacea* in and near Big Bend National Park, Cañon de Santa Elena Protected Area, and the Maderas del Carmen Protected Area.

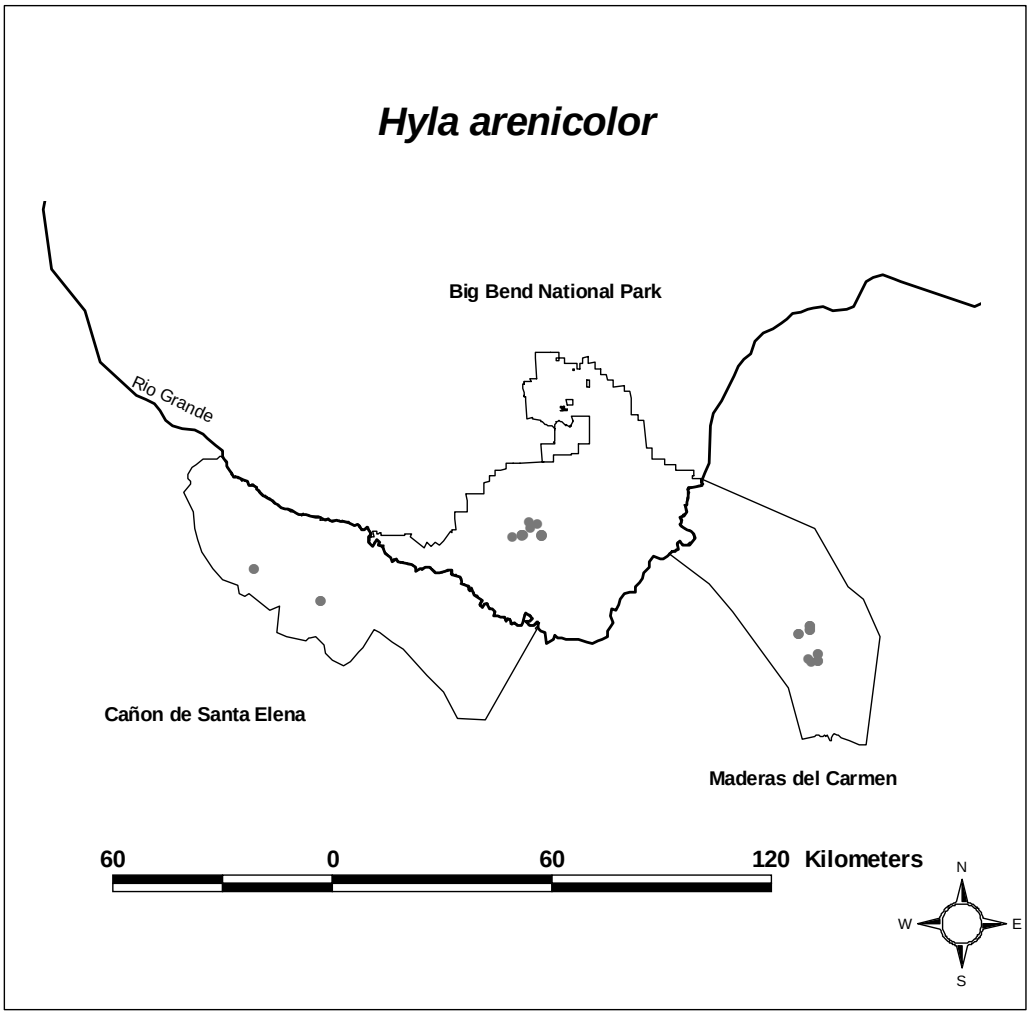

Figure 6. Localities of *H. arenicolor* throughout Big Bend National Park, Cañon de Santa Elena Protected Area, and the Maderas del Carmen Protected Area.

elevations of the Sierra Ricas and at Las Pilas. *Hyla arenicolor* were abundant and common throughout the higher elevation streams and rocky canyons in the Maderas del Carmen Protected Area. My collections in Cañon de Santa Elena Protected Area and the Maderas del Carmen Protected Area are significant in that these are new localities for this species and may represent range extensions.

Rana berlandieri (Fig. 7)—I found *R. berlandieri* to be common at the majority of permanent water sources throughout Big Bend National Park, Cañon de Santa Elena Protected Area, and the Maderas del Carmen Protected Area. I found this species at low-elevation and high-elevation sites including springs, along the banks of the Rio Grande River, stock tanks, and relatively large temporary water bodies.

Rana catesbeiana (Fig. 8)—This species is native to much of the central and eastern United States, ranging from Central Texas northeast to Maine (Conant and Collins 1998). This species has been introduced into the western United States (Stebbins 2003) and is non-native to the Big Bend Region (Dixon 2000). Throughout the western United States, *R. catesbeiana* have been implicated as a serious threat to native amphibians and reptiles (Schwalbe and Rosen 1988). In Big Bend National Park anecdotal accounts of calling *R. catesbeiana* at Rio Grande Village indicate that bullfrogs have been in the park since the early 1980's (Raymond Skiles pers. comm.; Big Bend National Park Natural History Field Observation Cards). The first known voucher specimen was collected from the Beaver Pond at Rio Grande Village in 1998. Since that time 9 other individuals have been collected, most of which were captured along the banks of the Rio Grande River from Lajitas to Rio Grande Village.

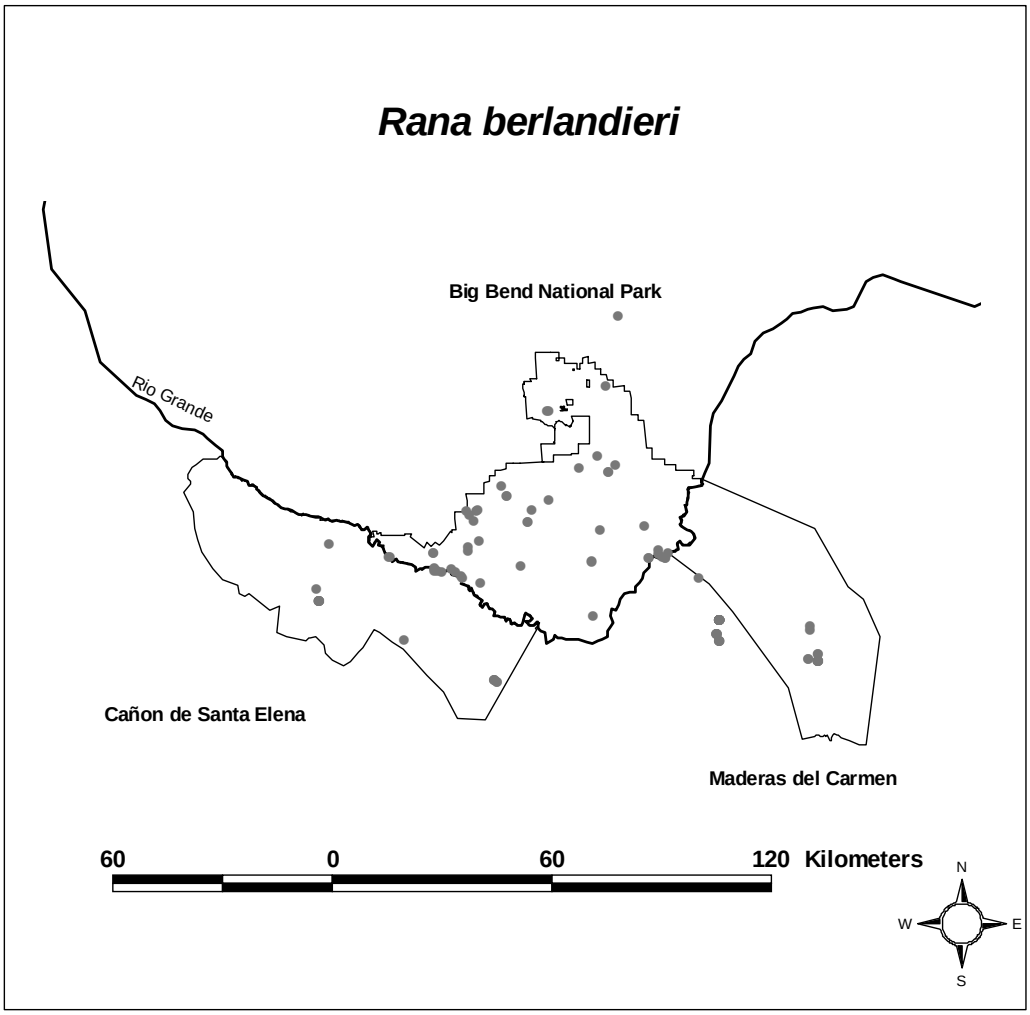

Figure 7. Localities of *R. berlandieri* in and near Big Bend National Park, Cañon de Santa Elena Protected Area, and the Maderas del Carmen Protected Area.

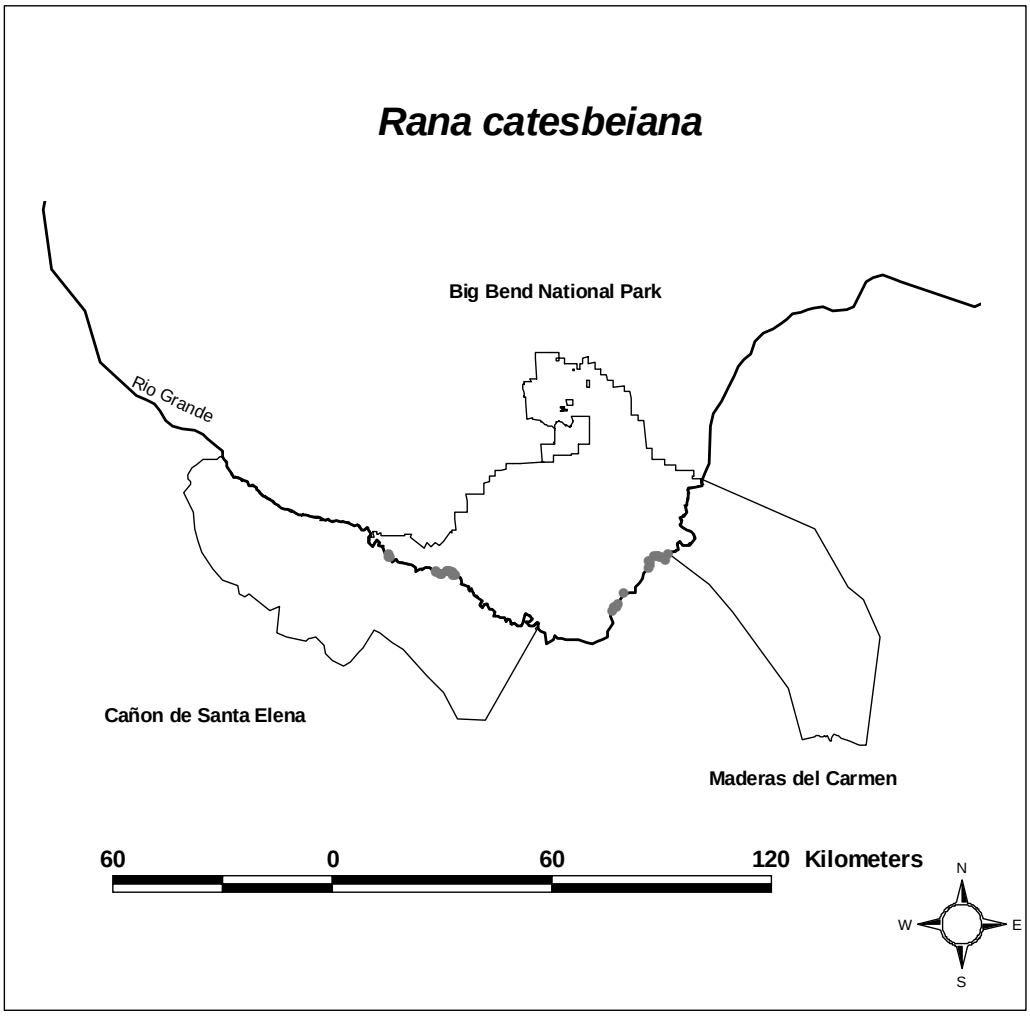

Figure 8. Localities of *R. catesbeiana* throughout Big Bend National Park, Cañon de Santa Elena Protected Area, and the Maderas del Carmen Protected Area.

I found *R. catesbeiana* on the banks of the Rio Grande River in Cañon de Santa Elena Protected Area but did not detect any in the Maderas del Carmen Protected Area. It should be noted that I did not survey the banks of the Rio Grande River within the Maderas del Carmen Protected Area and it is very likely that *R. catesbeiana* also occurs there. Bullfrogs do not seem to have moved into the interior of Big Bend National Park, Cañon de Santa Elena Protected Area, or Maderas del Carmen Protected Area. It may be that there is not suitable habitat away from the Rio Grande River, or that the terrestrial environment separating suitable aquatic habitat is inhospitable and restricts movement for this species. However, there are several permanent springs, large tanks, and lakes in the three protected regions that could support populations of *R. catesbeiana* if they were to become established. A feasible alternative hypothesis explaining the lack of this species in the interior of the three protected areas is that the introduction of *R. catesbeiana* into the region is relatively recent (as suggested by the fact that the oldest known voucher specimen is only 6 years old) and populations may be on the rise. If *R. catesbeiana* do colonize springs and tanks in interior regions within the protected areas, they will be very hard to eradicate and may pose a serious threat to native fauna.

Scaphiopus couchii (Fig. 9)—I found this species in all three protected areas. In Big Bend National Park *S. couchii* were found throughout the park, but tended to be in much greater abundance in the northern regions from Tornillo Flats to the northern park boundary. In Cañon de Santa Elena Protected Area *S. couchii* were found at a large stock tank along the road from San Carlos to Paso Lajitas. In the Maderas del Carmen Protected Area I found *S. couchii* in temporary pools in the lowland desert habitats.

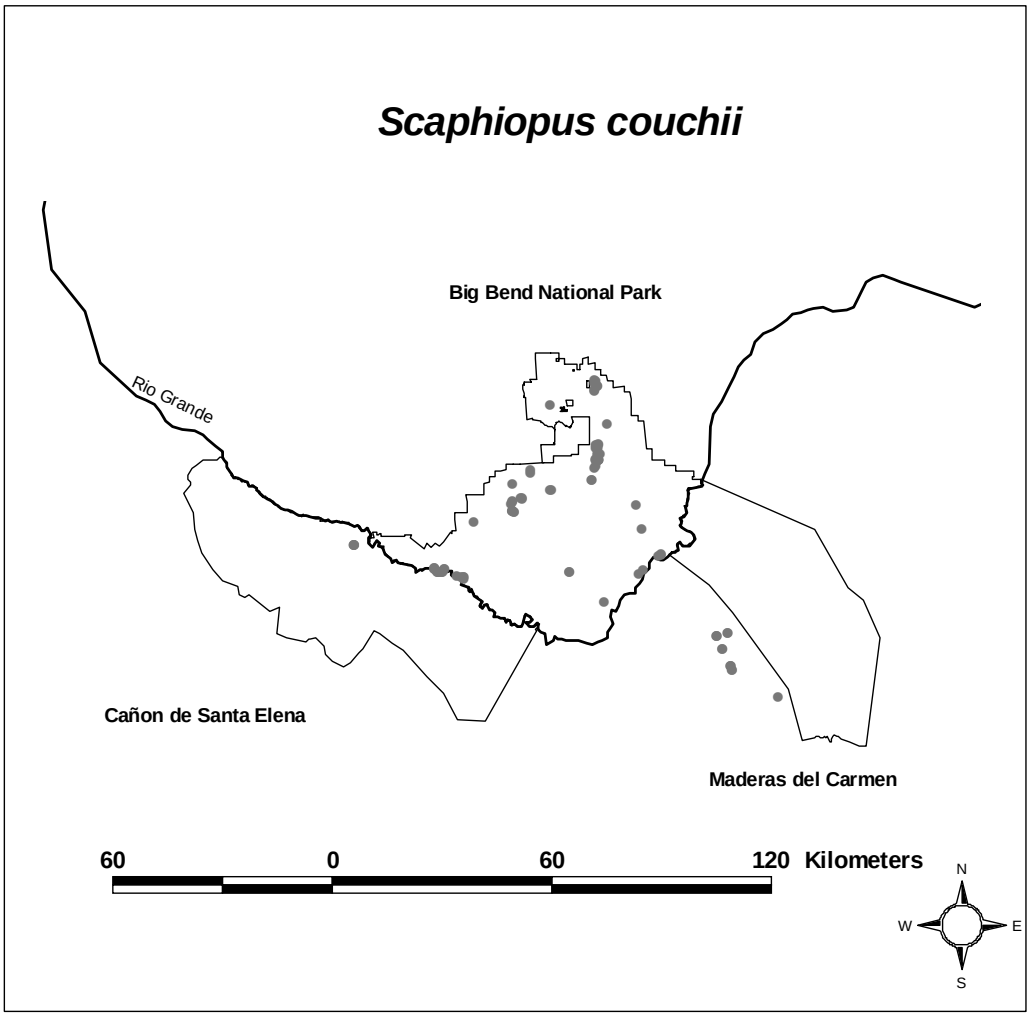

Figure 9. Localities of *S. couchii* in and near Big Bend National Park, Cañon de Santa Elena Protected Area, and the Maderas del Carmen Protected Area.

Although I only detected a few individuals of this species in the two Mexican protected areas, I observed ample suitable habitat (flat sandy clay loam soils) throughout the lowland desert regions of both areas. *Scaphiopus couchii* are common in areas where soils are frequently inundated and relatively high in clay content (Dayton et al., 2004). The fact that I did not detect many individuals of this species in the surveys is most likely because *S. couchii* are active only for very short periods after rain events and spend the remainder of the time beneath the surface.

Syrrhophus guttilatus (Fig. 10)—In Big Bend National Park the only historic records for *S. guttilatus* are from the Chisos Mountains. This species is believed to be a relict species in montane habitats in the Big Bend region. Over the past 7 years, extensive surveys of amphibians in Big Bend National Park have found *S. guttilatus* at several locations ranging from along the Rio Grande River (~700 m) to Boot Canyon (~2200 m). This species has direct development and does not require aquatic habitats for reproduction. Thus, they are not dependent on water and are able to inhabit a wide range of habitats. *Syrrhophus guttilatus* seem to be associated with rocky cliffs and talus slopes and, while individuals can be detected by listening for chorusing males, it is often difficult to capture them. Results from surveys in Big Bend National Park suggest that this species is likely to be much more common than previously thought. In Cañon de Santa Elena Protected Area I heard several individuals calling from the talus slopes at the downstream mouth of Santa Elena Canyon. None were detected in the Maderas del Carmen Protected Area. There is ample suitable habitat for this species

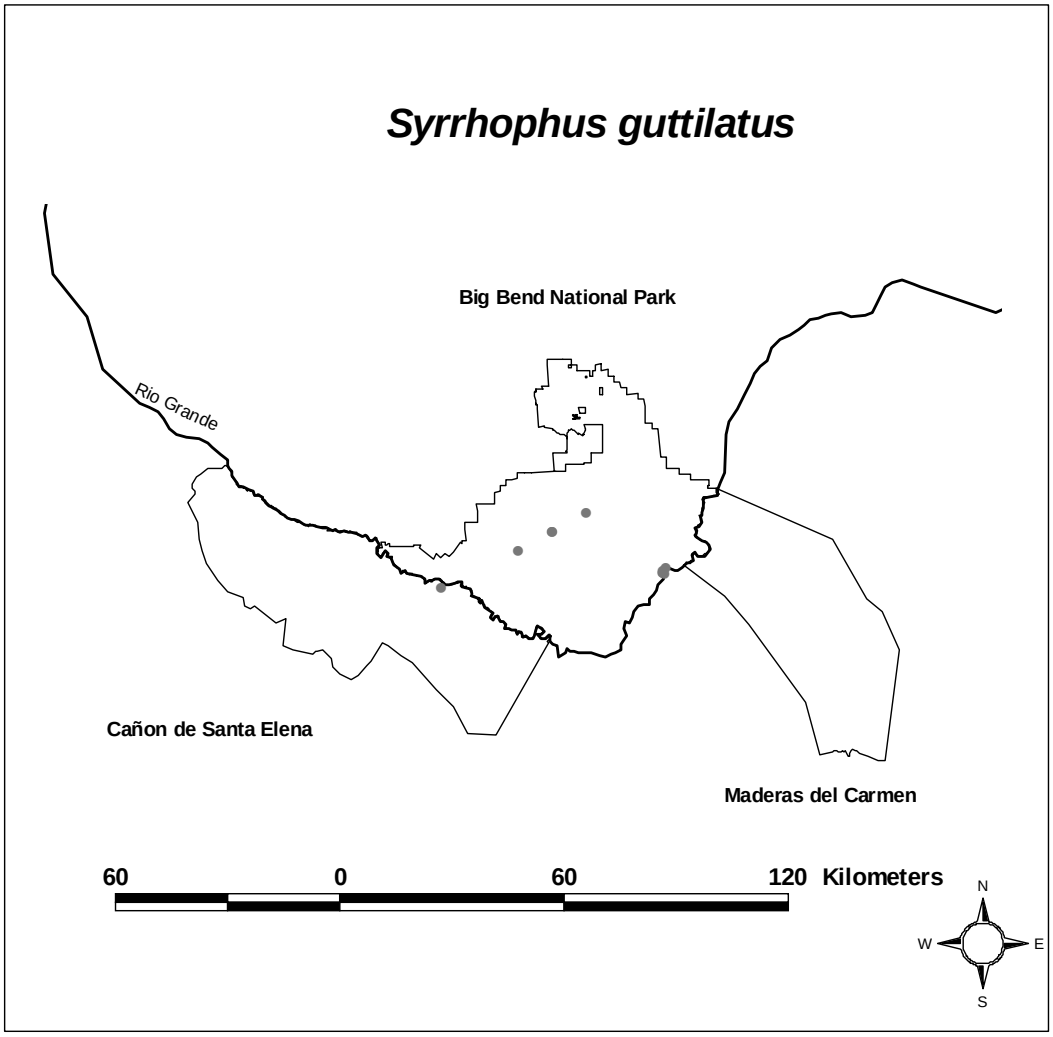

Figure 10. Localities of *S. guttilatus* throughout Big Bend National Park, Cañon de Santa Elena Protected Area, and the Maderas del Carmen Protected Area.

throughout both Cañon de Santa Elena Protected Area and the Maderas del Carmen Protected Area, and it is likely that *S. guttilatus* is distributed throughout both protected areas.

Spea multiplicata—This species has been reported from Big Bend National Park and Cañon de Santa Elena Protected Area. *Spea multiplicata* are common inhabitants of desert grasslands and can be readily found north of Big Bend National Park (Minton 1959, Conant and Collins 1998). There are only 6 known voucher specimens of *S. multiplicata* collected from Big Bend National Park, with the last known specimen being collected in 1990 (Table 3). My surveys of Cañon de Santa Elena Protected Area revealed very little habitat that I would classify as suitable for *S. multiplicata*. Extensive grasslands in the southeastern regions of Maderas del Carmen Protected Area may provide suitable habitat for *S. multiplicata*, however, none were detected during the surveys.

Bufo woodhousii—This species has been reported from Big Bend National Park and the Maderas del Carmen Protected Area, but it is believed to be relatively uncommon (Minton 1959). In Big Bend National Park there are only 10 known voucher specimens, all of which were collected from Rio Grande Village and the eastern mouth of Santa Elena Canyon (Table 3). The Big Bend region along the Rio Grande represents a finger-like extension of *B. woodhousii*'s range in southwestern Texas (Conant and Collins 1998). The fact that individuals have been collected along the Rio Grande in Big Bend National Park makes it likely that this species also occurred in Cañon de Santa Elena Protected Area and Maderas del Carmen Protected Area as well.

Table 3. Historical locations of *S. multiplicata* and *B. woodhousii* collected in Big Bend National Park, Texas.

Museum	Catalog #	Species	Exact Location	Date
TCWC	15906	*Spea multiplicata*	Tornillo Flat	8/03/1956
TCWC	15909	*Spea multiplicata*	Tornillo Flat	8/03/1956
BYU	2767	*Spea multiplicata*	Unspecified	7/22/1930
SRSU	1355	*Spea multiplicata*	8.6 Mi. W 385 on road Rosillos Mountains	9/8/1990
SRSU	1356	*Spea multiplicata*	8.6 Mi. W 385 on road Rosillos Mountains	9/8/1990
SRSU	1358	*Spea multiplicata*	8.6 Mi. W 385 on road Rosillos Mountains	9/8/1990
FMNH	27353	*Bufo woodhousii*	St. Helena Canyon	8/8/1937
FMNH	27354	*Bufo woodhousii*	Boquillas	8/11/1937
FMNH	27355	*Bufo woodhousii*	Boquillas	4/19/1905
KU	176140	*Bufo woodhousii*	Big Bend, Rio Grande Village	7/22/1966
TCWC	4241	*Bufo woodhousii*	Big Bend National Park	5/27/1944
TNHM	25622	*Bufo woodhousii*	Rio Grande River at Graham Ranch	4/27/1956
NMNH	103674	*Bufo woodhousii*	Boquillas	7/27/1937
MSB	40313	*Bufo woodhousii*	Big Bend National Park, Rio Grande Village	4/11/1968
MSB	20176	*Bufo woodhousii*	Rio Grande Campground, Big Bend National Park	4/12/1968
MSB	20166	*Bufo woodhousii*	Rio Grande Campsite, Big Bend National Park	4/19/1968

TCWC = Texas Cooperative Wildlife Collections, BYU = Brigham Young University, SRSU = Sul Ross State University, FMNH = Field Museum of Natural History, KU = Kansas University, TNHM = Texas Natural History Museum, NMNH = National Museum of Natural History, MSB = Museum of Southwestern Biology.

The last known voucher specimen from the Big Bend Region was collected in 1968 (Table 3). Over the past 7 years, extensive surveys have been conducted in the areas where *B. woodhousii* were historically collected, yet no individuals have been observed (Jung et al. 2002a, Dayton et al. 2004). This species likely bred in the flooded backwaters of the Rio Grande. Over the last century, the flow of the Rio Grande has been greatly reduced and the invasive *Arundo donax* (Giant Cane) has led to channelization of much of the riverbed. The combination of these two factors has significantly decreased the frequency and size of flood events along the Rio Grande. As a result, the potential breeding habitat for *B. woodhousii* has been greatly reduced. I feel that *B. woodhousii* no longer occurs in Big Bend National Park, Cañon de Santa Elena Protected Area, or the Maderas del Carmen Protected Area.

Discussion

The amphibian species assemblages were very similar among the three protected regions. Although I conducted relatively few sampling trips to Cañon de Santa Elena Protected Area and Maderas del Carmen Protected Area compared with Big Bend National Park, my findings are very useful to draw comparisons between the areas. Furthermore, these surveys are the most extensive surveys of amphibians in all three protected regions to this date and provide a baseline for future comparisons. I identified suitable habitat for several species that were not detected in one or more of the three regions. These species are: *B. woodhousii*, *S. multiplicata, R. catesbeiana*, and *S. guttilatus* in the Maderas del Carmen Protected Area, *S. multiplicata, B. debilis,* and *B.*

woodhousii in the Santa Elena Protected Area, and *S. multiplicata* and *B. woodhousii* in Big Bend National Park. Future surveys will undoubtedly add to the knowledge of species assemblages within the two Mexican Protected Areas. In fact CEMEX biologists are currently conducting biotic inventory work in the Maderas del Carmens which will likely increase the knowledge of the amphibian community in the Maderas del Carmens.

CHAPTER III

HABITAT SUITABILITY MODELS FOR DESERT AMPHIBIANS

Overview

A fundamental step in conserving biodiversity is identification of quality habitat needed to sustain populations of target species. I used large-scale environmental features to predict habitat suitability for four species of desert amphibians in Big Bend National Park, USA: *Scaphiopus couchii*, *Bufo punctatus*, *Bufo debilis*, and *Gastrophryne olivacea*. Model output was tested for reliability using data from 7 years of breeding site surveys. My models performed very well for predicting species occurrence. Suitable habitat for *B. punctatus* and *G. olivacea* extended over greater proportion of the study area compared to suitable habitat for *S. couchii* and *B. debilis*. My study provides the first habitat suitability model for desert amphibians and provides important information for conservation biologists and land managers concerned with preserving amphibian diversity in xeric landscapes.

Introduction

The distribution of organisms is clearly linked to habitat, hence identifying spatial relationships between organisms and environmental features is important for understanding autecology of species (Cowles 1899, Grinnell 1917). Moreover, understanding what environmental features predict species occurrence is important for development of successful conservation efforts (Pereira and Itami 1991, Akcakaya and Atwood 1997, Gibson et al. 2004). Species-environment correlations have been used to

predict the distribution of species across complex landscapes, in habitat suitability models (Verner et al. 1986, Guisan and Zimmermann 2000, Manly et al. 2002). Extrapolating from species-habitat relationships to predictive models of habitat suitability at the scale of landscapes helps elucidate factors that influence species persistence across broad spatial scales (Pereira and Itami 1991, Burnside et al. 2002, Root et al. 2003).

Landscape-level habitat suitability models have proven especially useful for predicting suitable habitat for organisms that are endangered, rare, or have a patchy distribution over space or time (Wu and Smeins 2000, Gibson et al. 2004). Many amphibian species, for example, are patchily distributed due to their tight association with wetlands, particularly in arid regions where suitable habitat is relatively sparse or fragmented (Dayton et al. 2004, Gray et al. 2004b). Amphibians with a free-swimming larval stage are dependent upon both suitable aquatic and terrestrial habitat. Although the presence of water and the suitability of the aquatic environment are critical components of amphibian habitat, amphibians are also dependent on specific terrestrial habitat components that provide refugia for adults. Thus, when identifying habitat suitability for amphibians it is essential to consider both terrestrial and aquatic habitat requirements (Pope et al. 2000, Hazell 2003, Porej et al. 2004). Adult frogs that burrow into the soil, for example, are less likely to persist in rocky areas regardless of whether aquatic habitats are present. Alternatively, if suitable aquatic environments are not present, the presence of suitable habitat for adults is unlikely to influence presence of the species in that area. As a result of this co-dependence of aquatic and terrestrial habitat

features, amphibians often occur in metapopulations because they rely upon multiple habitat types that do not always co-occur synoptically (Ray et al. 2002, Greenberg and Tanner 2005). This pattern is especially prevalent in landscapes where terrestrial habitat between breeding sites is unsuitable (Marsh and Trenham 2001).

Disruption or alteration of suitable habitat is well known to lead to increased isolation (spatially and genetically) among populations (Ficetola and De Bernardi 2004, Banks et al. 2005), and is believed to be one of the causes implicated in recent declines in amphibian populations throughout the world (Blaustein and Kiesecker 2002, Davidson et al. 2002, Brook et al. 2003). Habitat suitability models are applicable to amphibian conservation problems as they predict the probability distribution of suitable habitat, and thus provide a framework for management and research priorities (Storfer 2003). Although significant research and monitoring efforts over the past three decades have focused on factors influencing species assemblages and conservation issues of amphibians (Morin 1983, Heyer et al. 1994, Lips 2003, Lips et al. 2004, Stuart et al. 2004), factors that influence distributions, abundance, and persistence of amphibians in desert environments are relatively understudied (Woodward and Mitchell 1991). In the present study, I used environmental data in a geographical information system (GIS) to create predictive habitat suitability models for four amphibian species found in the Chihuahuan Desert: *Scaphiopus couchii* Baird, 1854 (Couch's Spadefoot Toad), *Bufo debilis* Girard, 1854 (Western Green Toad), *Bufo punctatus* Baird and Girard, 1854 (Red-spotted Toad), and *Gastrophryne olivacea* Hallowell, 1857 (Plains Narrow-mouthed Toad). The importance and applicability of habitat suitability models largely

depend upon whether models are tested for reliability (Ottaviani et al. 2004). To validate my models I compiled breeding site data from 7 years of field surveys to evaluate the accuracy of the models to predict suitable habitat for these species. The models provide important insight into environmental factors and spatial patterns that probably determine the species' distributions at coarse scales, and clearly serve as a useful conservation tool for the preservation of amphibian habitat in desert regions.

Methods

Study Area

My study area was Big Bend National Park (BBNP), which consists of approximately 800,000 acres, located in southwestern Texas along the Rio Grande River in the Chihuahuan Desert ecoregion (Fig. 1). Annual precipitation averages approximately 38 cm with nearly 75% of the rainfall occurring from May to September. Elevation ranges from 600 m along the Rio Grande River to nearly 2400 m in the Chisos Mountains, with most of the land between 762 and 1370 m. Mean summer and winter daytime temperatures are approximately 33^{o}C and 18^{o}C respectively, with extremes of 46^{o}C and – 4^{o}C. Creosote (*Larrea tridentata*) and lechuguilla (*Agave lechuguilla*) are the dominate the vegetation community over approximately 72% of the park (Plumb 1987). Major soil units are Lajitas-rock outcrop, Lozier-rock, Chamberino, and Chilicotol, together comprising approximately 69% of soils found in BBNP (Cochran and Rives 1985).

Spatial Data Layers

Variables included in my habitat suitability models were elevation, soil, slope, and proximity to drainage areas. Spatial data layers used were digital elevation models (DEM), digitized soil survey maps, and drainage maps. Digital elevation models (30 m resolution) were acquired from the Texas Natural Resources Information System (TNRIS), soil maps were obtained from digitized USDA soil maps of Big Bend National Park (Cochran and Rives 1985), and drainage/hydrology maps were obtained from the National Park Service. Spatial attributes (slope and buffer regions) were created using ArcView Spatial Analyst (ESRI, 1998). Data were converted to raster format and projected in NAD 83 with 30 m resolution. Geo-referenced data of breeding sites detected during field surveys were used to create GIS "species" layers.

Environmental Features Included in Suitability Models

Soil characteristics

Soil properties clearly influence the distribution of many amphibians species (Diller and Wallace 1999, Bradford et al. 2003, Dayton et al. 2004). Coarse-rocky soils have relatively low water holding capacity and drain quickly (Cochran and Rives 1985). These characteristics limit the duration water is available for breeding and hamper species ability to dig into the soil (Hardy 1945, Andersen et al. 2000). The capacity of a soil to hold available water (available water capacity) is expressed as inches of water per inch of soil. In BBNP available water holding capacities of soils range from 0.02 in/in (0.51 mm) in rocky areas to 0.21 in/in (5.33 mm) in clay loams (Cochran and Rives

1985). Soils with relatively high available water capacity are likely to be important for burrowing amphibians, as they provide moist refuge sites. In rocky terrain water will pool up in areas with slight depressions and may hold water for several months at a time. Although rock bound pools provide suitable habitat for amphibian larvae, habitat for adults is limited, especially for burrowing species. In BBNP many anuran species are strongly associated with specific soil types.

Slope

Steepness of a region significantly influences runoff. Some amphibian species are associated with habitats that have steep slopes (Diller and Wallace 1996, 1999), these species tend to inhabit permanent or long lasting streams in mountainous regions. In desert environments where accumulation of water is primarily a result of short lived thunderstorms, steep sloped regions provide relatively little area where water can accumulate to create potential breeding pools. Regions with low slopes provide more opportunities for water to pool up.

Elevation and proximity to drainages

Elevation is an important factor limiting the persistence of many amphibian species (Fauth et al. 1989, Bradford et al. 2003, Pineda and Halffter 2004). In BBNP there are no records of *S. couchii*, *B. punctatus*, *G. olivacea*, or *B. debilis* above ~1400 m (Dayton unpublished data). The majority of amphibians in BBNP inhabit areas with elevations ranging between 550 and 1000 m with the exception of *B. punctatus* which

has been found at higher elevations in the Chisos Mountains (Dayton 2001). Drainages, and areas in close proximity to them, receive runoff from seasonal floods. Runoff often pools up in drainages, as well as in back water flood areas, providing potential breeding habitat for amphibian species.

Model Framework

I assigned different suitability values to habitat categories based on published accounts and field observations of habitat associations for *S. couchii*, *B. debilis*, *B. punctatus*, and *G. olivacea*. Attributes for each habitat variable (i.e. specific soil type, slope category, etc.) were reclassified from 0-3 in ArcView. Higher numbers corresponded to more suitable habitat. GIS layers for each reclassified habitat variable were multiplied using the Map Calculator in ArcView to create a single landscape map. This is a multiplicative approach in which all layers are combined to create a single layer of all the habitat variables. The final step in creating the habitat suitability model was to reclassify the combined map into categories based on the value of each cell (Fig. 11).

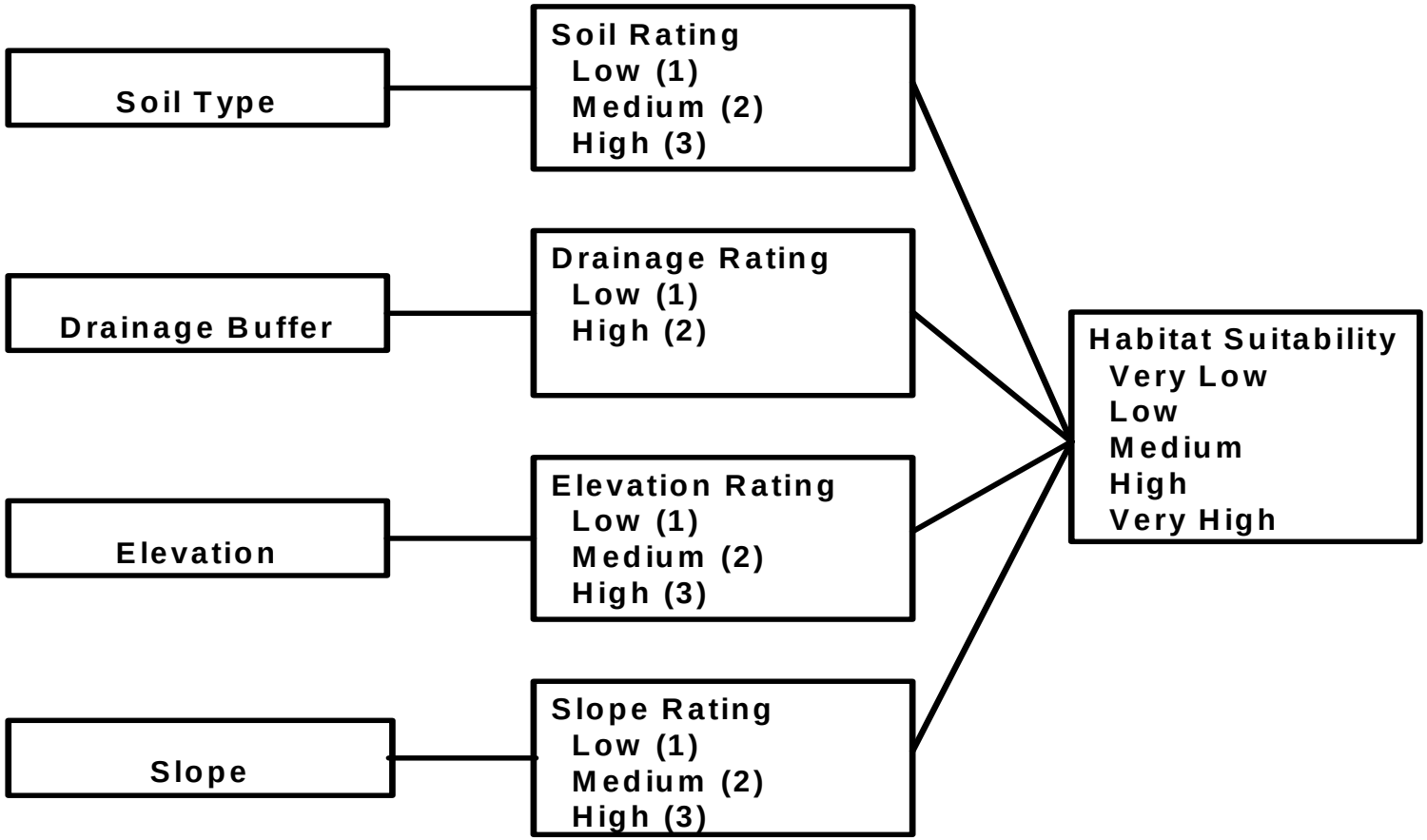

Figure 11. Criteria and structure used to develop habitat suitability models.

Thus, potential habitat suitability was determined by a combination of the landscape variables based on species specific habitat affinities. Some habitat features were ranked as 0 because species are not known to occur with that particular feature. For example, in BBNP *S. couchii* do not occur in the higher elevations of the Chisos Mountains, thus all elevation above 1200 m was ranked as 0. Because I used a multiplicative approach, all areas within BBNP that fell above 1200 scored 0 for potential habitat suitability irregardless of the other landscape level factors associated with that specific spot. The lowest predicted habitat suitability category was categorized as Very Low and the highest score as Very High. Intermediate scores were subdivided into three equal groups based on the combined scores of each habitat variable and categorized as Low, medium, and High. For each species I provide a detailed description on natural history affinities as well as a detailed compilation of how each habitat category was created for each species.

Scaphiopus couchii *and* Bufo debilis *habitat affinities*

Scaphiopus couchii and *B. debilis* are associated with similar habitats in BBNP (Dayton et al. 2004) and have comparable life histories. For these reasons I developed a single habitat suitability model that predicted suitable habitat for both species (Fig. 12). Both species are associated with clay loam soils and primarily breed temporary pools in alluvial floodplains (Strecker 1926, Newman 1987, Dayton et al. 2004). *Scaphiopus couchii* and *B. debilis* are extremely well adapted to living in desert environments. Both species can metamorphose in relatively few days, *S. couchii* in as little as 8 days

Landscape-Scale Model for *Scaphiopus couchii* and *Bufo debilis*

Soil Rating

3 High Likelihood
- Available water capacity > 0.10 In/in

2 Medium Likelihood
- Available water holding capacity > 0.08 In/in

1 Low Likelihood
- Available water holding capacity < 0.08 In/in

Slope Rating

2 High Likelihood
- Flat areas (slope < 3º)

1 Low Likelihood
- Moderate slopes (slope 3-6º)

0 Very Low Likelihood
- Steep slopes (> 6º)

Elevation

2 High Likelihood
- Low elevation (500-1000 m)

1 Medium Likelihood
- Medium elevation (1000-1200 m)

0 Very Low Likelihood
- High elevation (> 1200 m)

Possible environmental factor combinations

Elevation Rating	*Slope Rating*	*Soil Rating*	*Predicted Habitat Suitability*
0	**any**	**any**	**Very Low**
any	**0**	**any**	**Very Low**
1	**1**	**1 or 2**	**Low**
	2	**1**	**Low**
2	**1**	**1**	**Low**
1	**1**	**3**	**Medium**
	2	**2**	**Medium**
2	**1**	**2**	**Medium**
	2	**1**	**Medium**
1	**2**	**3**	**High**
2	**1**	**3**	**High**
	2	**2**	**High**
	2	**3**	**Very High**

Figure 12. Variable selection and criteria used to develop habitat suitability models for *S. couchii* and *B. debilis.*

(Mayhew 1965, Newman 1989) and *B. debilis* in as few as 20 days (Strecker 1926). In BBNP, *S. couchii* are distributed throughout the park with the greatest number of individuals occurring in the northern regions and near the Rio Grande River and at the lower elevations up to approximately 1200 m (Dayton 2001, Dayton et al. 2004). *Bufo debilis* occur primarily in the northern region of the park at elevations ranging from 700-900 m; however, a few individuals have been observed along the Rio Grande River and near the western park boundary at lower elevations (Dayton unpublished data). Both species and are relatively abundant where they occur (Strecker 1926, Minton 1959, Dayton et al. 2004). Adult *S. couchii* spend the majority of the year burrowed in the soil, only coming to the surface to breed and feed during seasonal rain storms (Mayhew 1965, Dimmitt and Ruibal 1980a, 1980b). Relatively little natural history information exists for *B. debilis*; though, they are also thought to burrow into the soil as well seek refuge beneath vegetation and rocks and in animal burrows (Creusere and Whitford 1976) (Dayton unpublished data).

Bufo punctatus *habitat affinities*

Bufo punctatus is associated with temporary and permanent water bodies throughout their range and breed in a wide variety of habitats including temporary bedrock pools, rocky canyons, low gradient flood plains, steeply sloped tributaries, and permanent springs (Fig. 13) (Mayhew 1965, Tevis 1966, Sullivan and Fernandez 1999, Bradford et al. 2003). Breeding primarily occurs following a rain event and continues for several weeks (Sullivan 1989). Although adults are believed to burrow and dig into

the ground during dry periods (Tevis 1966), they often take refuge beneath stones, vegetation, and other cover (Strecker 1926, Turner 1959). In BBNP, *B. punctatus* is distributed widely throughout the park (Dayton et al. 2004) and occur in a broad range of habitat types and elevation ranges but have not been found in the Chisos Mountains (Dayton et al. 2004).

Gastrophryne olivacea *habitat affinities*

Habitat criteria for *G. olivacea* were almost entirely based on my observations over 7 years of survey work (Fig. 14). *Gastrophryne olivacea* has been reported to be rare throughout BBNP; however, recent surveys indicate they are relatively common (Dayton unpublished data). Earlier reports of its scarcity are presumably due to secretive nature of this species, making it somewhat difficult to detect (Sullivan et al. 1996). Breeding takes place after seasonal rain storms and adults will continue to call for several days following a rain event (Dayton unpublished data). *Gastrophryne olivacea* are associated with a wide variety of habitats including stock tanks, tinajas, temporary pools, and frequently inundate alluvial floodplains (Smith 1934, Sullivan et al. 1996, Anderson et al. 1999). Adults seek refuge beneath fallen vegetation and rocks as well as within tarantula burrows (Fitch 1956, Dundee 1999, Dayton 2000). In BBNP, *G. olivacea* is distributed widely throughout the park and occur primarily in low and mid elevation ranges across a broad range of habitat types ranging from course rocky areas to clay loam flats (Dayton 2001) (Dayton unpublished data).

Landscape-Scale Model for *Bufo punctatus*

Soil Rating

3 High Likelihood
- Cobble

2 Medium Likelihood
- Gravel

1 Low Likelihood
- Sandy or fine

Slope Rating

2 High Likelihood
- Flat to moderate slopes (slope 0-6 º)

1 Low Likelihood
- Moderate to steep (slope 6-9º)

0 Very Low Likelihood
- Steep (> 9º)

Drainage Rating

2 High Likelihood
- < 50 m from drainage

1 Medium Likelihood
- > 50 m from drainage

Elevation Rating

1 High Likelihood
- < 1450

0 Very Low Likelihood
- > 1450

Possible environmental factor combinations

Elevation Rating	*Drainage Rating*	*Slope Rating*	*Soil Rating*	*Predicted Habitat Suitability*
0	**any**	**any**	**any**	**Very Low**
any	**any**	**0**	**any**	**Very Low**
1	**1**	**1**	**1 or 2**	**Low**
	2	**1**	**1**	**Low**
	1	**1**	**3**	**Medium**
	2	**1**	**2**	**Medium**
	2	**2**	**1**	**Medium**
	2	**1**	**3**	**High**
	2	**2**	**2**	**High**
	2	**2**	**3**	**Very High**

Figure 13. Variable selection and criteria used to develop habitat suitability models for *B. punctatus*.

Landscape-Scale Model for *Gastrophryrne olivacea*

Soil Rating

3 High Likelihood
- Cobble or available water capacity > 0.10 In/in

2 Medium Likelihood
- No cobble and available water holding capacity > 0.08 In/in

1 Low Likelihood
- No cobble and available water holding capacity < 0.08 In/in

Slope Rating

2 High Likelihood
- Flat to moderate slopes (slope 0-6 º)

1 Low Likelihood
- Moderate to steep (slope 6-9º)

0 Very Low Likelihood
- Steep (> 9º)

Elevation

2 High Likelihood
- Low elevation (500-1000 m)

1 Medium Likelihood
- Medium elevation (1000-1200 m)

0 Very Low Likelihood
- High elevation (> 1200 m)

Possible environmental factor combinations

Elevation Rating	*Slope Rating*	*Soil Rating*	*Predicted Habitat Suitability*
0	**any**	**any**	**Very Low**
any	**0**	**any**	**Very Low**
1	**1**	**1 or 2**	**Low**
	2	**1**	**Low**
2	**1**	**1**	**Low**
1	**1**	**3**	**Medium**
	2	**2**	**Medium**
2	**1**	**2**	**Medium**
	2	**1**	**Medium**
1	**2**	**3**	**High**
2	**1**	**3**	**High**
	2	**2**	**High**
	2	**3**	**Very High**

Figure 14. Variable selection and criteria used to develop habitat suitability models for *G. olivacea.*

Amphibian Surveys

During the summer months of May - August from 1998 to 2004 I conducted area-constrained surveys (patch sampling) (Jaeger 1994) at over 500 permanent and temporary water bodies throughout all of BBNP for the presence of amphibians. Sites ranged from ephemeral pools to permanent springs. Location of each site was recorded using a handheld Global Positioning System (GPS) unit. Site selection was determined based upon recent rain events. Due to the stochastic nature of rain events, random sampling of water bodies based on a grid-selection method would result in specific regions, and perhaps habitat types, being under-surveyed. Surveys were conducted over a 7-year period, and covered the range of available habitats throughout the entire study region. I used extensive dip-net sampling for tadpoles to document species presence. Dip-net surveys provide a good estimate of species presence (Shaffer et al. 1994) and are effective in detecting tadpoles even when densities are relatively low (Jung et al. 2002b). I excluded clay-lined cattle stock tanks from my analyses because although they may represent short term habitat for anurans tanks in BBNP, they filling and will soon be reverted back to natural conditions. Thus, tanks are unrepresentative of natural wetlands within BBNP. Tadpoles collected in the field were identified to species. Locality data for each species were recorded in DBF file format and converted to point shape files and then grid themes. Wetlands within 30 m of one another were grouped together as a single site.

Model Validation and Data Analysis

Validating the effectiveness of a habitat suitability model typically entails using independent data to test the ability of the model to accurately predict occurrence and or abundance of target species. Although I did not explicitly use data from my breeding site surveys to generate habitat suitability models, my observations on habitat affinities were used as one of the factors in weighing the model variables. Accuracy of the model was tested by overlaying GIS species layers onto predicted habitat suitability maps. I then used chi-square goodness-of-fit tests to examine whether the observed frequencies of occurrence in each habitat category were different than would be expected if the number of breeding sites simply reflected the availability of each predicted habitat category. To determine which habitat categories were drivers of significant differences, I compared 95% confidence intervals for the proportions of used, versus available, predicted habitat categories (Bonferroni adjusted):

$$o_i - Z_{(1-\alpha/2k)} \sqrt{o_i(1-o_i)/n} \leq \pi_i \leq o_i + Z_{(1-\alpha/2k)} \sqrt{o_i(1-o_i)/n}$$

This method evaluates whether the observed proportions of individuals in a specific habitat category fall outside the predicted 95% confidence interval for that habitat category (Neu et al. 1974, Manly et al. 2002).

To estimate habitat selection functions (*sensu* Manly et al. (2002), I calculated selection probabilities using the following formula:

$$\hat{w}_i = o_i/\pi_i,$$

where $\hat{w}_i$ is the selection ratio for habitat category i, o_i is the proportion of the sample of used resources in category i, and π_i is the proportion of available resources units that are in category i. Values were then standardized using their (Manly et al. 2002) standardized selection ratio:

$$B_i = \hat{w}_i / (\sum_{i=1}^{I} \hat{w}_j)$$

This calculation provides the standardized relative probability (B_i) of selection for a particular habitat category based on a scale of 0 to 1.

Results

Scaphiopus couchii

Predicted suitable habitat for *S. couchii* is scattered throughout BBNP, with the majority of Very High quality habitat occurring in the north western region of the park (Fig. 15). Approximately 76% of all *S. couchii* breeding sites detected during my surveys occurred in High and Very High habitat suitability categories (Table 4). Breeding sites occurred in predicted habitat categories disproportionately than would be expected if they occurred in the categories relative to their availability ($\chi^2 = 353$, df =4, $P < 0.0001$). *Scaphiopus couchii* occurred in the Very High category significantly more frequently than expected, less frequently than expected in Very Low categories and there were o significant differences for the Medium and High categories (Table 4).

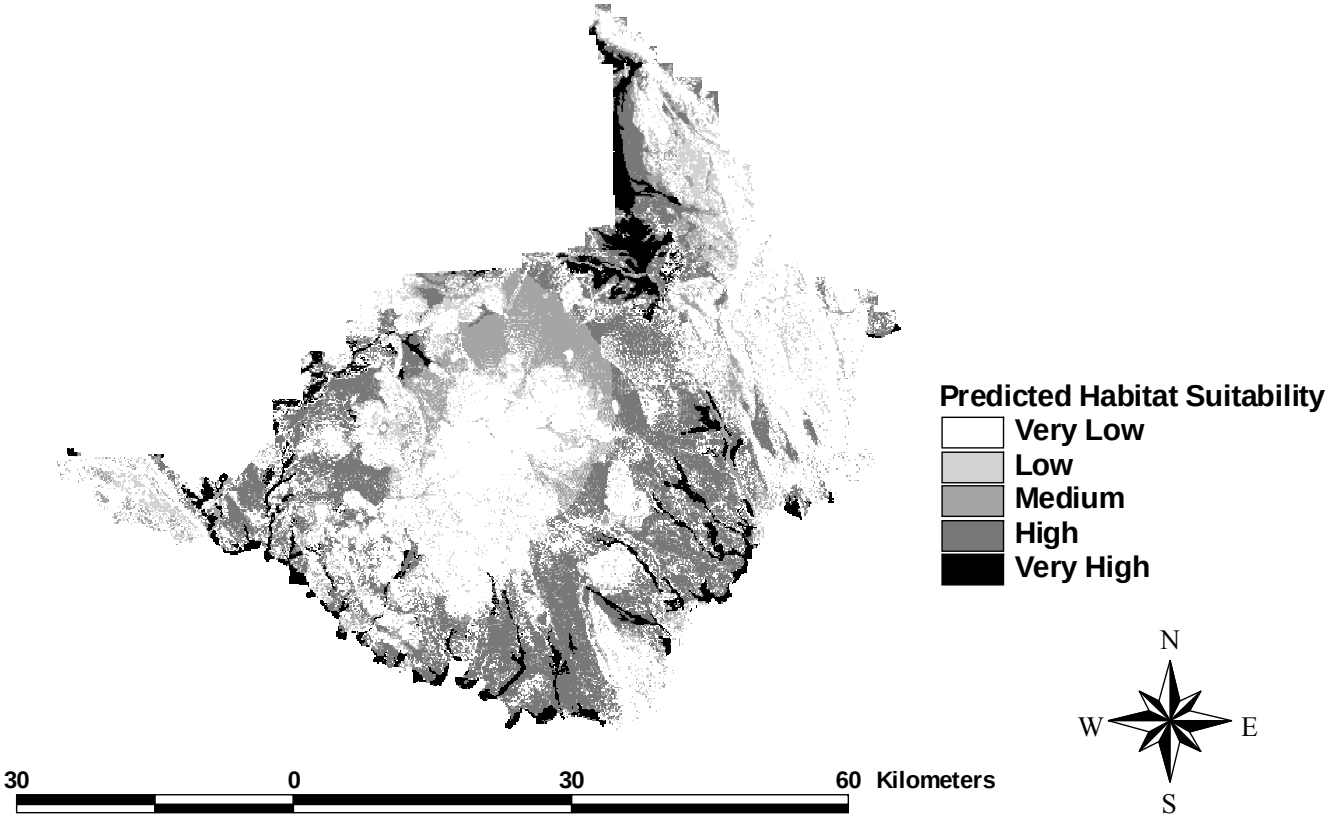

Figure 15. Predicted habitat suitability for *S. couchii* and *B. debilis* in Big Bend National Park, Texas.

Table 4. Occurrence of, and habitat selection indices for, *S. couchii*, *B. debilis*, *G. olivacea*, and *B. punctatus* in each of the five predicted habitat categories.

Species	Predicted habitat category (i)	Proportion of total area of each predicted habitat (π)	Observed # of individuals in each habitat category (u)	Expected # of individuals in each category (πu^{+})	Proportion individuals in each habitat category (o)	Selection index ($\hat{w}$)	Standardized selection index (B)	Confidence intervals (Bonferroni adjusted)
S. couchii	Very Low	**0.46***	9	40	0.10	0.22	0.02	$0.02 \leq p_1 \leq 0.19$
	Low	**0.09***	2	9	0.03	0.23	0.02	$-0.02 \leq p_2 \leq 0.06$
	Medium	0.16	10	14	0.11	0.70	0.07	$0.03 \leq p_3 \leq 0.20$
	High	0.21	16	18	0.18	0.88	0.08	$0.08 \leq p_4 \leq 0.29$
	Very High	**0.07***	50	6	0.57	8.72	0.84	$0.44 \leq p_5 \leq 0.70$
B. debilis	Very Low	**0.46***	1	12	0.04	0.08	0.01	$-0.03 \leq p_3 \leq 0.10$
	Low	0.10	0	3	0	0	0	N/A
	Medium	0.16	2	4	0.08	0.47	0.03	$-0.01 \leq p_3 \leq 0.16$
	High	0.21	0	5	0	0	0	N/A
	Very High	**0.07***	23	2	0.88	13.42	0.96	$0.78 \leq p_5 \leq 0.99$
G. olivacea	Very Low	**0.36***	3	17	0.06	0.17	0.04	$-0.03 \leq p_2 \leq 0.15$
	Low	0.06	1	3	0.02	0.39	0.08	$-0.03 \leq p_2 \leq 0.07$
	Medium	0.13	4	6	0.09	0.65	0.14	$0.02 \leq p_3 \leq 0.19$
	High	0.20	11	9	0.23	1.16	0.25	$0.08 \leq p_4 \leq 0.39$
	Very High	**0.25***	28	12	0.60	2.37	0.50	$0.42 \leq p_5 \leq 0.78$
B. punctatus	Very Low	**0.36***	15	36	0.15	0.42	0.06	$0.02 \leq p_2 \leq 0.29$
	Low	0.11	0	11	0.16	1.50	0.20	$0.03 \leq p_2 \leq 0.30$
	Medium	0.26	25	25	0.38	1.45	0.20	$0.20 \leq p_4 \leq 0.56$
	High	0.24	45	24	0.25	1.00	0.14	$0.09 \leq p_5 \leq 0.40$
	Very High	0.04	13	2	0.06	3.02	0.41	$-0.03 \leq p_5 \leq 0.15$

*Significant at $P < 0.05$ after Bonferroni corrections; u^{+} = Total number of individuals of each species.

Bufo debilis

Predicted suitable habitat for *B. debilis* is scattered throughout BBNP, with the majority of Very High quality habitat occurring in the north western region of the park (Fig. 15). Approximately 89% of all *B. debilis* breeding sites detected during my surveys occurred in the Very High habitat suitability category (Table 4). Breeding sites occurred in predicted habitat categories disproportionately than would be expected if they occupied the categories relative to their availability (χ^2 = 240, df =4, P < 0.0001). *Bufo debilis* occurred in the Very High category significantly more frequently than expected, less frequently than expected in the Very Low category, and no *B. debilis* were found in the Very Low and High categories (Table 4).

Bufo punctatus

Predicted suitable habitat for *B. punctatus* is widely distributed throughout BBNP, with the majority of Very High quality habitat occurring throughout the southern regions of BBNP but with large patches scattered throughout the entire park (Fig. 16). Breeding sites occurred in predicted habitat categories disproportionately than would be expected if they occurred in the categories relative to their availability (χ^2 = 102, df =4, P < 0.0001). Approximately 31% of all *B. punctatus* breeding sites occurred in High and Very High habitat suitability categories (Table 4). More *B. punctatus* individuals occurred in Very High habitat categories than expected; however the results were no

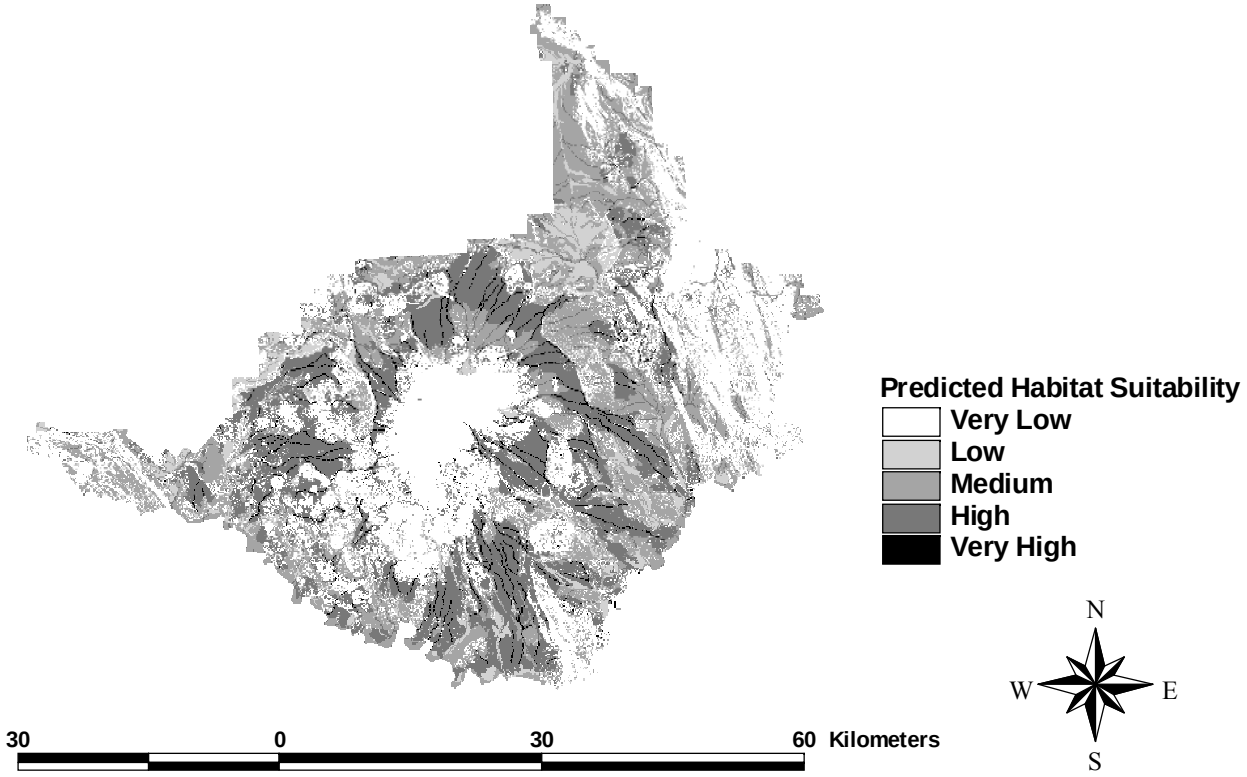

Figure 16. Predicted habitat suitability for *B. punctatus* in Big Bend National Park, Texas.

significant (Table 4). The only significant difference detected was for the Very Low category, where fewer individuals occurred than expected (Table 4).

Gastrophyrne olivacea

Predicted suitable habitat for *G. olivacea* is scattered throughout BBNP, with the majority of Very High quality habitat occurring in the northern and eastern regions of the park with isolated patches throughout the southern and western boundaries (Fig. 17). Approximately 83% of all *G. olivacea* breeding sites detected during my surveys occurred in High and Very High habitat suitability categories (Table 4). Breeding sites occurred in predicted habitat categories disproportionately than would be expected if they occurred in the categories relative to their availability ($\chi^2 = 35$, df =4, $P < 0.0001$). *Gastrophryne olivacea* occurred in the Very High category significantly more frequently than expected, less frequently than expected in the Very Low category, and there were no significant differences in the Low, Medium, and High categories (Table 4).

Discussion

My study is the first habitat suitability model for desert amphibians. By utilizing species-specific habitat associations for larvae and adults, I was able to accurately predict suitable and non-suitable habitat for 3 of the 4 amphibian species. I validated the models with data from breeding site surveys obtained over a 7 year period. Model validation demonstrated that habitat suitability models performed well for predicting

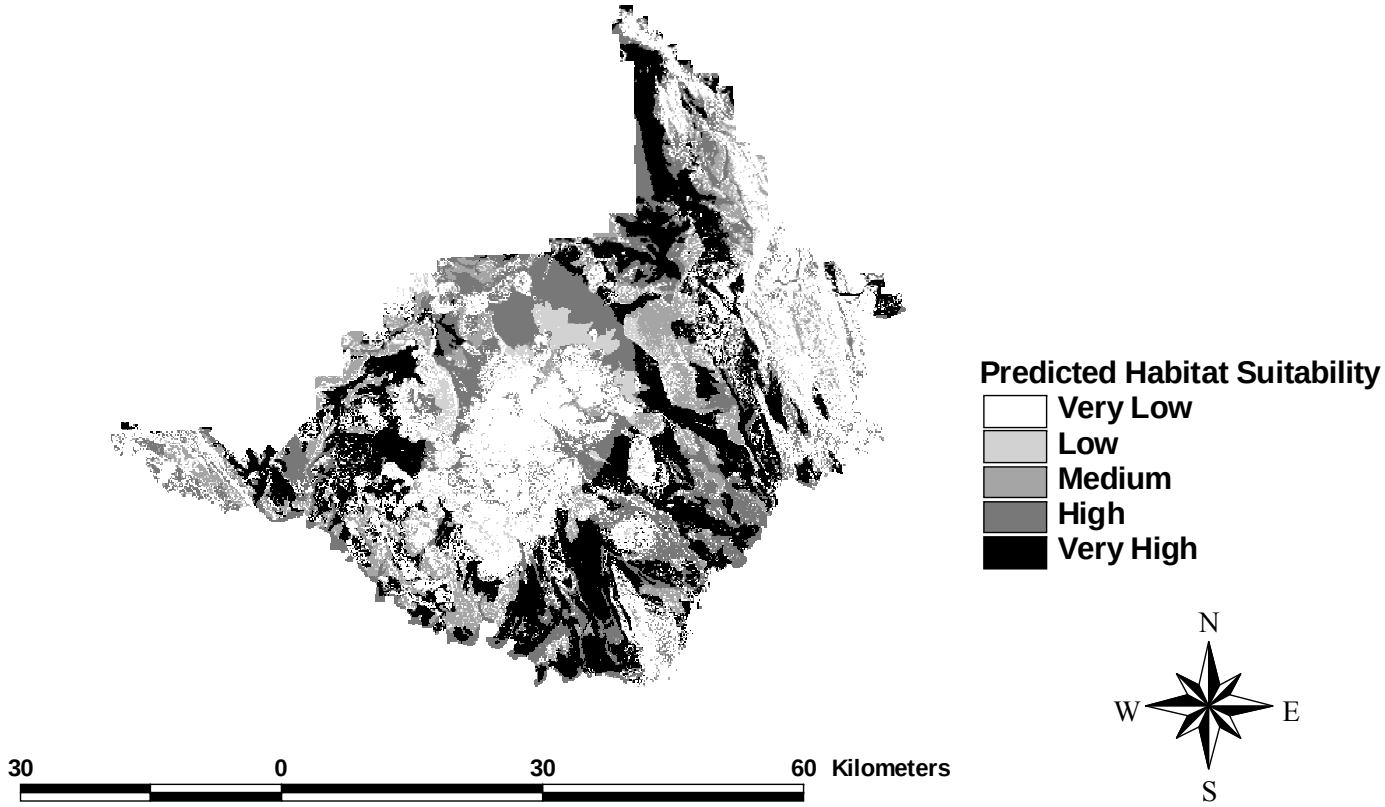

Figure 17. Predicted habitat suitability for *G. olivacea* in Big Bend National Park, Texas.

species occurrence in Very High suitable habitat categories and species absence in Very Low Habitat suitability categories for *S. couchii*, *B. debilis*, and *G. olivacea,* but not for *B. punctatus*. The inability of my model to predict the presence or absence of individuals of all species in many of the intermediate predicted habitat categories indicates that my models perform best in discriminating between Very Low and Very High predicted habitat categories. This discrepancy is likely to the coarseness of my model input (e.g. small pockets of potential habitat may exist within areas I classified as low quality habitat), inaccuracies in GIS data (e.g. modeled slope values may not correspond perfectly to slope on the ground), an artifact of small sample sizes in some regions, or an inaccuracy in my initial categorization of the habitat variables. Although I did not systematically sample the entire park, I did cover the representative regions over the 7 year period. Thus, I feel that the inconsistencies in the intermediate habitat categories are likely either due to inaccuracies in my ratings of the habitat variables or the coarseness and accuracy of the GIS data.

Very High and High suitable habitat categories for *G. olivacea* and *B. punctatus* extended over greater areas of BBNP compared to *S. couchii* and *B. debilis*. Suitable habitat for *S. couchii* and *B. debilis* was limited primarily to the northern regions of the BBNP and along the Rio Grande River, with fingers of Very High quality habitat extending into the interior of the park. *Gastrophryne olivacea* and *B. punctatus* also occurred in these areas, as well as in regions with rocky substrata and steeper slopes. The fact that the model performed poorly for *B. punctatus* is likely due to the fact that *B. punctatus* utilize a wide variety of habitats and may not be as restricted in their habitat

use by large scale environmental features as the other 3 species. The data used in my models may be too coarse to pick up small scale environmental features that may actually be suitable habitat for *B. punctatus.*

Habitat suitability models with validation, such as I presented here, can be used to generate testable hypotheses about distributions of amphibians in relationship to large-scale environmental features. For many amphibian species that inhabit desert environments suitable habitat is relatively sparse and patchily distributed. Thus, populations may be isolated by unsuitable xeric regions. Furthermore, amphibian populations in desert environments are likely to exhibit significant fluctuations in size over time due to the unpredictability of aquatic habitats. Desert amphibians in general often do not breed on an annual basis due to unpredictable environmental conditions (Bragg 1945), commonly lose entire clutches due to desiccation (Mayhew 1965, Tevis 1966, Newman 1987), have extremely low juvenile survivorship rates (Creusere and Whitford 1976), are susceptible to predation in all stages of their development (Newman 1987, Dayton and Jung 1999, Bonine et al. 2001, Dayton and Wapo 2002), and often persist in isolated populations (Turner 1959, Mayhew 1965). Combined, these factors presumably lead to frequent extinction events at local breeding sites. Species persistence over the long term relies upon recolonization from neighboring sites (Hanski 1987, Rustigian et al. 2003). It follows then, that the ability of amphibians to move between isolated populations is largely dependent on the suitability of habitat among populations (Marsh and Trenham 2001, Gray et al. 2004a, Gray et al. 2004b). Thus,

regions with high quality terrestrial and aquatic habitat are likely to provide a source of emigrants that maintain satellite populations.

Implications for Conservation

An important implication of the habitat suitability models is that high quality habitat facilitates movements among isolated breeding sites. Therefore, protecting areas where high quality habitat is abundant should positively influence the persistence of local populations that depend on the dynamics of local extinction and colonization (Vos and Stumpel 1996, Marsh et al. 1999, Green 2003). This is particularly important for species such as *S. couchii* and *B. debilis* that had patchily distributed areas of high quality habitat that were often isolated from one another by significant distances. Whereas *B. punctatus* and *G. olivacea* seem to be habitat generalists and persist in a relatively broad range of habitats. The variation in the predicted suitable habitat among these four functionally similar species (i.e. xeric-adapted amphibians) elucidates that fact that developing single species habitat suitability models is a more appropriate approach then trying to develop to multi-species models which assume species will respond to changes in habitat in a similar manner (Lindenmayer et al. 2002). The fact that I used field surveys to test my models significantly increases their usefulness and relevance for conservation and management purposes as I have provided evidence that these models work (Fleishman et al. 2001, Pullin and Knight 2001, Pullin et al. 2004). I am optimistic these results will be very useful to BBNP resource managers. Although it is important to realize the scope of this study was constrained within the boundaries of

BBNP, the framework of my model provides a valuable tool for land managers and conservation biologists interested in determining suitable habitat for other xeric adapted amphibians.

CHAPTER IV

PRIORITY EFFECTS AND DESERT ANURAN COMMUNITIES

Overview

The roles of priority effects and predation in structuring anuran communities have not been considered important in desert environments characterized by highly ephemeral pools and anuran species that breed synchronously. Predation is one mechanism that can set the stage for priority effects to be important, especially in ephemeral pools where resources are limiting and densities are high. I observed oophagy by *Scaphiopus couchii* tadpoles on *Bufo speciosus* eggs in the field, and conducted laboratory experiments to test the hypothesis that *S. couchii* tadpoles would reduce *B. speciosus* survivorship via predation. Three-day old *S. couchii* tadpoles reduced hatching success of *B. speciosus* eggs by nearly 90%. When *S. couchii* and *B. speciosus* eggs were laid the same day, *S. couchii* tadpoles reduced *B. speciosus* egg survivorship by 56%. Results indicate priority effects and predation may play an important role in influencing species composition of anuran assemblages in desert regions. My study provides more support for the need to re-evaluate the current paradigm in aquatic ecology that suggests predation does not play a role in structuring community assemblages in temporary pools.

Introduction

A central goal in ecology is to understand what determines ecological patterns among species across space and time (MacArthur 1968), and steady progress has been made toward understanding abiotic and biotic factors that determine the structure of communities in very different settings (Hutchinson 1959, Dayton 1971, Belyea and Lancaster 1999). The general consensus is that so-called "assembly rules" vary from system to system, and different communities may operate under different "rules" (Simberloff 2004). In aquatic environments a paradigm of community assembly has emerged that is based on the interplay between hydroperiod, resource competition, and predation (Morin 1983, Woodward 1983, Wellborn et al. 1996). The result of this interplay largely determines which species may be present or absent at a given site. Communities of larval anurans fit well into this paradigm of community structure. Pools with short hydroperiods are utilized by species with short larval periods and rapid development and in general tend to be low in species richness in comparison to longer lasting sites (Babbitt and Tanner 2000, Snodgrass et al. 2000). Species that inhabit ephemeral pools generally tend to be superior competitors, but very susceptible to predation (Woodward 1983, Dayton and Fitzgerald 2001). At the other end of the spectrum, species with relatively long larval periods require sites that persist long enough for metamorphosis to occur. However, pools with longer hydroperiods are colonized by predators, and the species with longer larval periods deal much better with predation. Hence, the balance between hydroperiod, predation, and competition appears to explain how tadpole communities are structured.

How well does the anuran community assembly paradigm apply to species that breed in highly ephemeral environments? In desert regions, the majority of anuran species breed in short-lived ephemeral pools that are created by unpredictable seasonal thunderstorms (Sullivan 1989, Woodward and Mitchell 1991), and tend to exhibit behavioral, developmental, and morphological adaptations that enable them to persist in harsh environments. In xeric environments, anurans congregate in temporary pools following a rain event and exhibit explosive breeding behavior (Sullivan 1989). Importantly, there is very little temporal segregation of breeding among species compared to temperate regions where groups of species tend to breed asynchronously over a several month period (Woodward and Mitchell 1991). The lack of asynchronous breeding in desert regions is presumably due to the fact that pools with short hydroperiods do not last long enough for sequential use of the site by different species, or cohorts of the same species. As a result desert anurans tend to be synchronous breeders breeding over a few day period centered on individual rain events. Additionally, factors such as predation that are associated with regulating species persistence in temperate and tropical environments (Morin 1986, Petranka et al. 1994) were thought not to be important in highly stochastic and ephemeral environments (Woodward and Mitchell 1991). However, empirical evidence from the few studies that have examined the roles of predation on eggs and tadpoles of desert anurans does suggest that predation may be an important mechanism affecting anuran community structure in temporary pools (Newman 1987, Dayton and Fitzgerald 2001, Dayton and Wapo 2002). Results from these studies suggest that “assembly rules” regulating

community composition of amphibians in temperate and tropical regions may also be important in determining the structure of amphibian communities in desert regions. Petranka and Kennedy (1999) showed that tadpoles readily consume macro-invertebrates as well as other amphibians and suggest that predation may be very important in structuring temporary pond communities.

One process that has not been explored as a mechanism of community assembly in desert anurans is priority effects, the advantages that early-arriving species, or species that hatch sooner, may have over latecomers in an assembling community. In temperate regions where species often tend to breed asynchronously, early arrivals have a potential competitive and predatory advantage over "late" arriving species (Travis 1983, Alford and Wilbur 1985, Petranka et al. 1994). In communities with asynchronous breeding, early breeders may deplete resources for "late" arriving species and grow to sizes that enable them to prey upon eggs and tadpoles of late breeders thereby inhibiting their population growth or entirely prohibiting their colonization. In breeding pools where tadpoles vary in age and size both intra and inter specific oophagy has been suggested as a mechanism for how predation may structure amphibian communities (Banks and Beebee 1987, Marshall et al. 1990, Tejedo 1991, Petranka and Kennedy 1999).

Oophagy by one species on another may affect community composition by altering densities, or even presence of species in the community. Being the first to breed should reduce the potential for predation on eggs and tadpoles by conspecifics and other species (Petranka and Thomas 1995). Two potential benefits of oophagy have been postulated. First, egg consumption reduces the number of future competitors, thus

reducing resource depletion (Crump 1983). Second, oophagy provides a high energy food source (Drewes and Altig 1996, Kam et al. 1998, Gibson and Buley 2004). These "benefits" may be especially important in ephemeral pools where resources are limited and tadpole density is high. Indeed, experiments have shown that supplementation of food and lower densities of tadpoles increased the probability of metamorphosis as well as the size of new *Scaphiopus couchii* (Couch's Spadefoot) metamorphs (Newman 1987, 1989)

In the Chihuahuan Desert, anuran species that use ephemeral breeding sites are not randomly distributed (Dayton and Fitzgerald 2001). Tadpoles of *S. couchii* have the shortest larval period and rarely occur with tadpoles of other species. Pair-wise experiments showed tadpoles of *S. couchii* were more susceptible to predation presumably because of their high activity level (Dayton and Fitzgerald 2001). This pattern fit the paradigm of anuran community assembly and helped explain lack of co-occurrence of larval anuran species across the Chihuahuan Desert landscape. However, I did not rule out other biotic mechanisms, such as oophagy, that may also influence the co-occurrence of species.

Here I show results of experiments using *S. couchii* tadpoles and *Bufo speciosus* (Texas Toad) eggs to test the hypothesis that a species with a relatively fast developmental rate (*S. couchii*) will consume eggs and reduce the survivorship of a species with a slower developmental rate (*B. speciosus*). Specifically, I examine the role of oophagy as a mechanism resulting in non-random associations of *S. couchii* and *B.*

speciosus across the Chihuahuan Desert landscape in Big Bend National Park, Texas, USA.

Methods

Study Area and Organisms

Big Bend National Park is located in southwestern Texas along the Rio Grande in the Chihuahuan Desert Ecoregion. Annual precipitation averages 35 cm with approximately 70% of the rainfall occurring from May to September (Brown 1994). Summer rains occur primarily as isolated downbursts which flood arroyos and create breeding pools. The two species used in this study, *S. couchii* and *B. speciosus*, are explosive breeders that use temporary pools created by summer monsoon storms (Bragg 1945). *Scaphiopus couchii* typically call during the first night of a rain (Sullivan 1989), whereas *B. speciosus* will call for up to four days after a rain event (Moore 1976). Eggs are deposited in temporary pools that last from a few days to several months. *Scaphiopus couchii* deposit their eggs in gelatinous strings surrounding submerged vegetation, a single female will deposit several egg masses throughout a pond. As little as 30 hrs is needed for *S. couchii* eggs to hatch and time to metamorphosis can be as quick as 8 days (Newman 1987), the shortest of any North American anuran (Buchholz and Hayes 2000). *Bufo speciosus* lay eggs in thin strings at the base of submerged vegetation, often in a single locality within the pool. In Big Bend I have observed up to 7 amplecting pairs depositing eggs at the base of a single submerged plant. *Bufo speciosus* eggs require approximately 2-3 days to hatch and tadpoles reach

metamorphosis in 18 – 60 days (Wright and Wright 1949, Moore 1976). These two species are regionally sympatric; however, they show very little overlap in their use of breeding sites (Dayton and Fitzgerald 2001).

Laboratory Experiments

In July 2003 I collected *S. couchii* tadpoles and eggs and *B. speciosus* eggs from two ephemeral pools in Big Bend National Park, Texas. The two pools differed in hydroperiod and species composition. The first pool filled on July 5 and had only *S. couchii* tadpoles that hatched on July 6. The second pool filled on July 7 at which time *S. couchii*, and *B. speciosus* were heard chorusing. On July 8 I collected *S. couchii* tadpoles from the first pool and *B. speciosus* and *S. couchii* eggs from the second pool. Tadpoles and eggs were housed in separate 40-liter buckets. On July 9 I set up an experiment to test for differences in survivorship of *B. speciosus* eggs reared with *S. couchii* tadpoles from two age classes. The experiment was a completely randomized design consisting of three treatments: a control group of 30 eggs of *B. speciosus* with 5 *S. couchii* tadpoles enclosed in a 2-mm mesh cage (no access to eggs); an experimental group with 30 *B. speciosus* eggs (N = 20; Gosner stage $\bar{x}$ = 15.9, SD = 0.22) and 5 newly hatched *S. couchii* tadpoles (N = 20; length $\bar{x}$ = 7.05 mm, SD = 0.22 mm; Gosner stage $\bar{x}$ = 23, SD = 0.10), and an experimental group with 30 *B. speciosus* eggs and 5 3-day old *S. couchii* tadpoles (N = 20; length $\bar{x}$ = 15.4 mm, SD = 0.37 mm; Gosner stage $\bar{x}$ = 32.95, SD = 0.21). Eggs and tadpoles were randomized among treatments and

treatments were replicated 10 times. Tadpoles and eggs were placed in plastic tubs (30 cm x 15 cm x 8 cm deep) filled with one liter of aged tap water. Experiments were terminated after 36 hours when the first *B. speciosus* eggs hatched. This design enabled me to examine the variation in survivorship of *B. speciosus* eggs when reared with *S. couchii* tadpoles of different age and size classes, while controlling for potential indirect effects that presence of *S. couchii* tadpoles may have on hatching success of *B. speciosus* eggs (i.e. the caged tadpoles in the control group). I used analysis of variance (ANOVA) followed by Tukey's post hoc tests to test the hypothesis that egg survival differed among the three treatments. Percent survivorship data for each tub was Arcsine square root transformed prior to analysis to meet assumptions of normality.

Results

Field Observations

On four occasions over the past four years I observed *S. couchii* and *B. speciosus* breeding in the same pool. In these instances *S. couchii* eggs hatched first and thousands of *S. couchii* tadpoles swarmed the *B. speciosus* egg strings, biting and consuming *B. speciosus* eggs. Gosner stages of the *S. couchii* tadpoles at the four sites ranged from 25 to 40 (Gosner 1960). The disparity in Gosner stages among sites was due to the variation in developmental rates and time of oviposition. In all 4 cases survivorship of *B. speciosus* was notably reduced as inferred by the lack of viable eggs. In two of the pools zero *B. speciosus* metamorphs were observed indicating that oophagy by *S. couchii* may have completely eliminated those cohorts of *B. speciosus.*

Experimental Results

S. couchii tadpoles in both experimental treatments consumed the eggs of *B. speciosus*. There were significant differences in the survivorship of *B. speciosus* eggs among the treatments ($F_{2,27} = 96.88$, $P < 0.00001$). Tukey's tests revealed significant differences between all treatments ($P < 0.05$). An average of 97% of *B. speciosus* eggs hatched in the control group (n = 10, $\bar{x} = 0.97$, SD = 0.02), significantly more than the two treatment groups ($P<0.0001$). Hatching success was also significantly different between the two experimental treatments ($P = 0.001$), with 44% (n = 10, SD = 0.17) of *B. speciosus* eggs hatching that were reared with small *S. couchii* tadpoles and 13% (n = 10, SD = 0.04) of the eggs raised with large *S. couchii* tadpoles hatching (Fig. 18).

Discussion

Both inter and intra-specific oophagy has been reported in several anuran species, and it is postulated that oophagy plays a role in regulating species co-occurrence in temperate environments (Petranka et al. 1994). *Scaphiopus couchii* tadpoles significantly reduced survival of *B. speciosus* eggs. *Scaphiopus couchii* tadpoles had a greater effect on *B. speciosus* egg survivorship when there was a lag period of a few days between hatching of the two species. Yet, even when hatching was offset by less than 24 h, *S. couchii* tadpoles significantly reduced *B. speciosus* egg survivorship via oophagy. My laboratory experiments combined with field observations support the hypothesis that *S. couchii* tadpoles are effective predators on *B. speciosus* eggs.

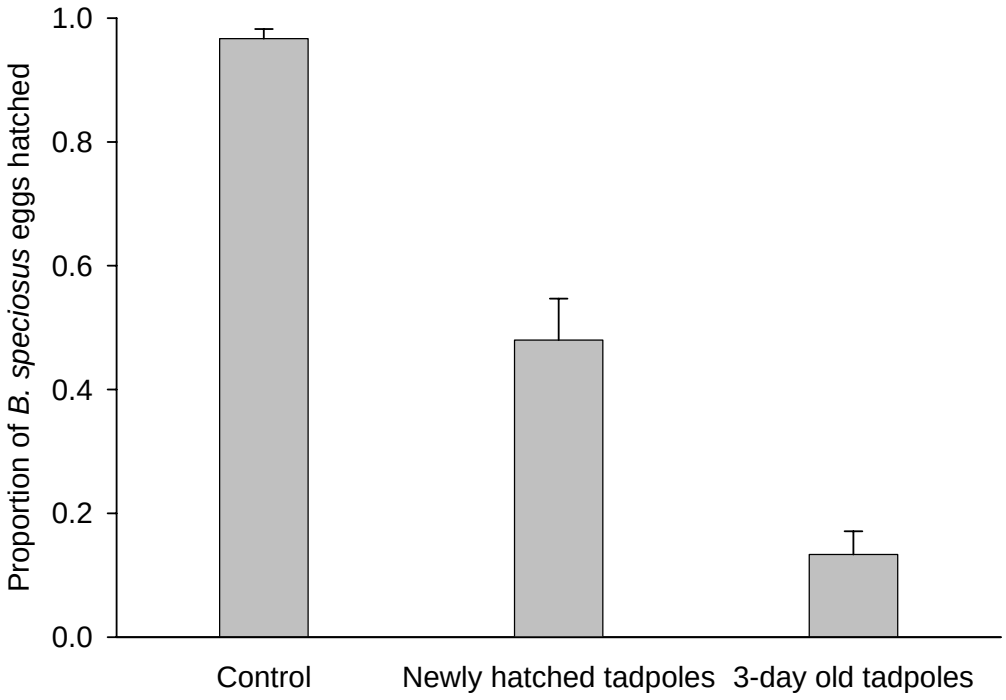

Figure 18. Proportion of *B. speciosus* eggs that hatched in each of the three treatments.

It has been suggested that high rates of oophagy has led to evolution of synchronized breeding in some systems (Petranka and Thomas 1995). The rationale is that explosive breeding reduces age and size variation among individuals in the tadpole community and should therefore reduce oophagy. In fact, studies examining oophagy have shown that "late arriving" anurans avoid using breeding pools where "early arriving" species are already present (Banks and Beebee 1987, Petranka et al. 1994).

Interestingly, my results imply that oophagy is also important in a synchronous breeding community. *Scaphiopus couchii* and *B. speciosus* are explosive, synchronized breeders, yet there is sufficient variation in developmental rates to allow oophagy to manifest important effects on survival and density of species. The rapid development of *S. couchii* tadpoles creates a gap in Gosner stage (Gosner 1960) and size among species of co-occurring tadpoles. The short period between egg deposition and hatching provides *S. couchii* tadpoles with a potential competitive and predatory advantage over other species that require longer periods from egg deposition to hatching. In the Chihuahuan Desert landscape, the fast-growing *S. couchii* and relatively slower *B. speciosus* are functional analogs of early and late-arriving species in asynchronous breeding anuran communities.

The benefits of oophagy to *S. couchii*, and associated costs to *B. speciosus* further set the stage for priority effects in structuring the Chihuahuan Desert anuran community, especially when resources are limiting. Increased size and decreased time to metamorphosis of *S. couchii* tadpoles in low density food supplemented treatments in Newman's (1987) experiments, suggest that resources are limited and that high densities

lead to longer larval periods which can be catastrophic in short lived pools where the primary cause of mortality is desiccation. In natural pools where densities of *S. couchii* tadpoles are often high and resources are limited (Newman 1987), the added nutrition provided by eggs and corresponding reduction in density of *B. speciosus* may increase the likelihood of *S. couchii* tadpoles successfully reaching metamorphosis.

Due to the short-lived nature of ephemeral pools and synchronous breeding of anurans (Woodward and Mitchell 1991), the roles of priority effects and predation in structuring desert anuran communities have been somewhat overlooked (but see Newman, 1987; Dayton and Fitzgerald, 2001; Dayton and Wapo, 2002). My results suggest that in the Chihuahuan Desert anuran community, resource limitation and variation in developmental rates facilitate oophagy by *S. couchii* on *B. speciosus*. The effects of oophagy on use of breeding sites by species, or cohorts, may be important in structuring amphibian communities in desert environments. My results combined with the limited studies examining the importance of predation risk in ephemeral pools suggest that, as Petranka and Kennedy (1999) suggest, it is time to rethink the hydroperiod gradient theory that states predation is not an important mechanism structuring community composition of ephemeral pools.

CHAPTER V

PREDATOR NAIVETE ENHANCES COHORT SURVIVAL IN A XERIC-ADAPTED ANURAN

Overview

Direct and indirect effects of predators play an important role in influencing species persistence and the composition of many ecological communities. The impact predators have on prey behavior, growth, and survival is dependent upon prey defenses and the susceptibility of prey to predators. I tested the hypothesis that organisms that inhabit short-lived, species-poor, aquatic environments will be predator-naïve and highly susceptible to predation. I examined multiple effects of predators on tadpoles of a xeric-adapted anuran, Couch's Spadefoot Toad (*Scaphiopus couchii*), that inhabit highly ephemeral pools in desert environments. I conducted laboratory and mesocosm experiments to test for non-lethal and lethal effects of predators on activity, development, growth, and survival of *S. couchii* tadpoles. Chemical cues of predators elicited no response in behavior, development, or growth. Direct effects of predators significantly decreased survivorship and as result of prey thinning, time to metamorphosis was accelerated. I suggest that in short-lived environments, where predator presence is rare, prey are likely to be predator-naïve and to exhibit little or no response to the presence of predators. As a result, direct numerical effects of predators can be either catastrophic on prey populations by eliminating every individual, or may actually increase overall survival via thinning of prey populations that results in an

increase in per capita resources for surviving individuals. Although predators are relatively rare in highly ephemeral aquatic environments they may play an important role in facilitating the long-term persistence of their prey.

Introduction

Predators play an important role in structuring the composition of many species assemblages (Paine 1974, Sih et al. 1985, Hero et al. 1998, Crooks and Soule 1999). The negative impact of predators on individuals is relatively clear-cut: the fitness of individuals that are killed is zero. However, when members of a cohort are killed by predators, surviving individuals can benefit by reaping the benefit of increased per capita resources (Paine 1969, Fauth and Resetarits 1991, Vonesh 2005). Predators may also facilitate increased species diversity by reducing competitive interactions among prey species, *sensu* the Keystone predator effect Paine (1966), Estes et al. (1998), and Fauth (1999). However, they can also entirely restrict species from utilizing a particular environment (Bohonak and Whiteman 1999, Knapp et al. 2001, Reiger et al. 2004). As a result, most organisms have behavioral and morphological adaptations that enable them to co-exist with predators. Species that have been subjected to constant predation pressure over many generations tend to evolve fixed defenses such as spines, cryptic coloration, noxious toxins, and low activity levels that are present regardless of whether predators are present or absent. Fixed defense mechanisms are presumed to be costly because resources that could be allocated to increased fecundity, or other fitness traits, are shunted towards predator defenses. An alternative strategy to fixed defenses is to

allocate energy only towards defense mechanisms when faced with predation risk. Plasticity in behavior, morphology, and development is common in many organisms that experience fluctuating environments and varying exposure to predators (Sih 1980, Sih 1986, Lima and Dill 1990, DeWitt et al. 2000, Relyea and Werner 2000, Resetarits 2001, Kunert et al. 2005). Altering behavior or morphology in response to predators often incurs costs such as reduced growth (Johansson et al. 2001, Relyea 2002a, Dahl and Peckarsky 2003, Teplitsky et al. 2003) and lower fecundity (Black and Dodson 1990, DeWitt 1998, Dixon and Agarwala 1999). Although predator-induced defenses increase survivorship, organisms must balance the conflicting demands between growth and the costs of predator-induced responses (Sih et al. 2003)

Both fixed and plastic defense traits can be considered adaptive if the trait results in increased survivorship and ultimately greater fitness. Alternatively, if a species has evolved in a predator-free environment, or the costs of defense mechanisms outweigh fitness gains, I would expect no fixed or plastic defense responses to predators and, thus, very high mortality rates when predators are present (Sih et al. 2000). In fact, populations of organisms never exposed to new kinds of predators (predator-naïve) are often decimated by exotic predators (Case and Bolger 1991, Fritts and Rodda 1998, Knapp and Matthews 2000). Such examples of invasive predators are somewhat unique in that prey organisms are faced with novel predators and anti-predator defenses have little time to evolve.

Freshwater aquatic environments encompass a wide variety of habitats ranging from species-poor ephemeral sites to long-lasting or permanent sites that support high

species diversity and greater proportions of predatory species (Wellborn et al. 1996, Spencer et al. 1999, Babbitt et al. 2003). Organisms that utilize short-lived sites tend to be very active in order to maintain relatively high feeding rates to facilitate rapid growth (Woodward 1983, Suhling et al. 2005). Rapid growth is necessary in ephemeral habitats as delaying development time greatly increases the risk of death due to desiccation (Newman 1987, Suhling et al. 2005). The cost of high activity rates is that although activity is correlated with increased growth rates (Relyea and Werner 1999), it is also correlated with susceptibility to predation (Werner and Anholt 1993, Skelly 1994, Wissinger et al. 1999, Suhling et al. 2005). Susceptibility to predation may not be as ecologically important to species inhabiting ephemeral sites where predator diversity is low compared to longer-lasting sites (McPeek 1990, Wellborn et al. 1996, Spencer et al. 1999). In long-lasting aquatic environments where predator richness is high, prey species exhibit behavioral and morphological traits that enable them to avoid predators (Morin 1983, Woodward 1983, Dayton et al. *In press*). Importantly, the qualities that permit species to be successful in one habitat may restrict them from inhabiting different habitats, and result in distinct communities across environmental gradients (Wellborn et al. 1996, Wellborn 2002). Based on these ecological premises, I can predict generalized prey characteristics along the hydroperiod gradient (Fig. 19).

The numerical direct effects of predators on prey are expected to be greatest when prey densities are high and resources are low; whereas the indirect effects of

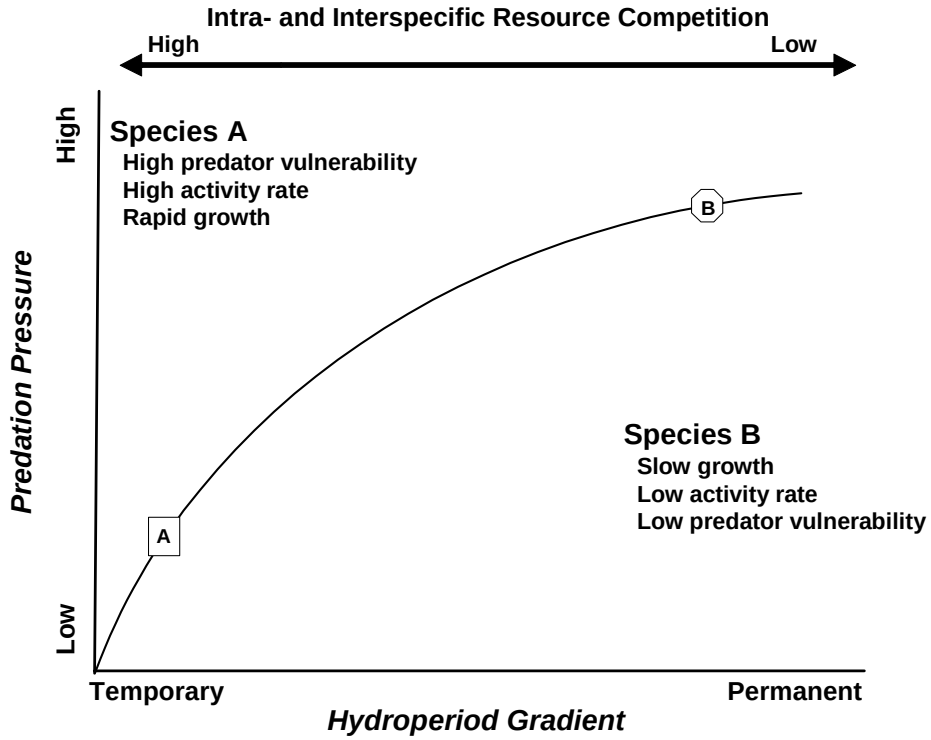

Figure 19. Relationship of predation pressure, competitive environment, and hydroperiod gradient with predictions of prey characteristics along the gradient (adapted from Wellborn et al. 1996). I expect species A to be highly susceptible to predation and show few defensive traits in the presence of predators because the cost of altering behavior and growth in delaying developmental time are too great in sites where desiccation is the primary cause of death. As a consequence of high susceptibility to predation, species A should be excluded from sites with long hydroperiods and high predator loads. Species B exhibits predator-induced defenses in the presence of predators. As a result, developmental times are longer, and Species B is excluded from short lived pools.

predators (e.g., decreased growth as a result of behavioral or morphological responses to predators) should be greatest in environments where resources are abundant (Van Buskirk and Yurewicz 1998). Non-lethal responses to predators via induced changes in growth play important roles in determining species persistence and the assemblage of natural communities (Peacor and Werner 2001, Binckley and Resetarits 2003, Resetarits et al. 2004). For organisms inhabiting highly ephemeral pools where pond desiccation is the primary cause of death and resources are limited, the associated costs of reduced growth as a consequence of modifying behavior may be too high (e.g. reduced growth and delayed time to maturity or metamorphosis results in death by desiccation). When predators occur with organisms that lack fixed or plastic defense mechanisms, prey suffer high mortality rates. Although predators negatively impact the fitness of their victims, both theoretical and empirical studies have shown that predators can have a positive influence on surviving individuals due to increased per capita resources as a result of the thinning of the prey population (Morin 1983, Fauth 1990, Abrams and Rowe 1996). However, it is important to consider that the costs of plasticity in behavior and growth resulting from non-lethal predator cues may be so high that potential benefits of predator-avoidance are outweighed. This imbalance between costs of defense mechanisms and potential benefit can even exist when prey densities are low (Resetarits et al. 2004). Thus, in stable aquatic environments where predator densities are high and relatively constant, I would expect prey to have numerous defense mechanisms, whereas in unpredictable, short-lived, aquatic sites where predators are uncommon and resources limited, I would expect little or no response of prey to the presence of predators.

I tested the hypothesis that organisms that inhabit short-lived, species-poor, aquatic environments should be predator-naïve and highly susceptible to predation. Specifically, I examined multiple effects of predators on tadpoles of a xeric-adapted anuran, *Scaphiopus couchii* (Couch's Spadefoot Toad). I used a combination of laboratory and mesocosm experiments to test two separate, but related, hypotheses regarding the impact predators have on tadpole survivorship and species persistence throughout the landscape. Because *S. couchii* utilize extremely ephemeral environments and pond desiccation is the primary cause of death for most cohorts of *S. couchii* larvae, I hypothesized that predators would not cause lower activity rates or alter the growth patterns of tadpoles. This hypothesis should be supported if the *S. couchii* tadpoles were either predator-naïve or the costs of altering behavior and development outweigh the gains. I further hypothesized that direct numerical effects of predators on tadpoles would facilitate growth of surviving individuals due to increased available resources resulting from the thinning of tadpole densities.

Methods

Study Area and Organism

Big Bend National Park is located in southwestern Texas in the Chihuahuan Desert Ecoregion. Annual precipitation averages 35 cm with approximately 70% of the rainfall occurring from May to September (Brown 1994). Summer rains occur primarily as isolated downbursts. The species used in my study, *S. couchii*, is one of the most xeric-adapted anuran species in the world. Adults spend the majority of their life buried

beneath the desert floor, coming to the surface for short periods during seasonal rains to breed in ephemeral pools (Mayhew 1965, Dimmitt and Ruibal 1980a, 1980b), and typically call only during the first night of a rain (Sullivan 1989). Eggs are deposited in ephemeral pools that usually last for only a few days. As little as 30 hrs is needed for eggs to hatch and time to metamorphosis typically takes 7-10 days (Mayhew 1965, Newman 1987, Morey and Reznick 2000), the shortest of any North American anuran (Buchholz and Hayes 2000).

Effects of Predators on Growth and Development

I collected *S. couchii* eggs from three ephemeral pools in Big Bend National Park, Texas < 24 hr after they were deposited. Eggs were combined and placed into a single plastic swimming pool (1.2 m diameter, 0.3 m tall, filled with ~40 gallons of aged tap water) that was housed in the laboratory. Two days post-hatching (N = 10; length $\bar{x}$ = 10.8, SD = 0.78 mm; Gosner stage (Gosner 1960) $\bar{x}$ = 25, SD = 0), I set up an experiment to test for the effects that chemical cues of predators and alarm cues of injured prey have on development (time to metamorphosis), growth (tadpole size), and behavior (activity). I chose these variables as they are surrogates for anuran fitness (Berven 1990) and are plastic defense traits common in many aquatic species (Laurila et al. 1998, Lardner 2000, Bryan et al. 2002, Relyea 2004). The experiment was a completely randomized design consisting of three treatments: a control group where tadpoles were reared without predators, a "non-lethal" experimental group where

tadpoles were reared with a caged predatory beetle larvae (Insecta: Hydrophilidae), and a "lethal" experimental group where tadpoles were reared with a caged Hydrophilid beetle larvae that was fed 5 *S. couchii* tadpoles on a daily basis. Predators were enclosed in a 2-mm mesh cage that prevented access to tadpoles but permitted water exchange between predator cages and the rest of the experimental arena. Control tubs also had cages (no predators) to control for potential cage effects. All predators were starved for at least 48 h prior to being placed in cages. Eight tadpoles were placed in plastic tubs (30 cm x 15 cm x 8 cm deep) filled with one liter of aged tap water. Tadpoles were randomized among treatments and treatments were replicated 10 times. A fixed diet of crushed TetraMin® tropical fish flakes of 15 mg/day/tadpole was maintained throughout the study. Food rations were not limiting and food was present in tubs throughout the experiment. These rations are consistent with other laboratory studies that have reared *S. couchii* tadpoles (Morey and Reznick 2000). Water was changed on day 3 and 6. Beetle larvae that did not consume tadpoles within a few hours were replaced. I chose to use Hydrophilid beetle larvae as the predator, as they are common throughout the study region and are very effective predators on *S. couchii* tadpoles in the field (Newman 1987).

Every two days I preserved one tadpole from each tub in order to compare growth (total length) and development (Gosner stage) among treatments throughout the experiment. This method enabled me to test for differences in growth and development at several intervals while not having to take multiple measurements on an individual tadpole. Experiments were terminated after 8 days when the first tadpoles reached

Gosner stage 42 (emergence of forelimbs). There were four removal periods: three during the experiment and one at the end of the experiment. The final removal consisted of 5 tadpoles per tub. In seven of the tubs one or more tadpoles died during the experiment (Control = 2; Non-lethal Cue = 3; and Lethal Cue = 2). These tubs were removed from all analyses as tadpoles in these tubs had access to more resources per capita, which could influence growth and development. Seven tadpoles were damaged in preservation; these were also excluded from analyses. I used analysis of variance (ANOVA) to test for differences in growth and development among treatments at each of the four intervals. Because I removed tadpoles throughout the experiment, I was able to examine the variation in development across all treatments at several different time periods. This method enabled me to test for effects at every stage of the experiment and thus examine potential ontogenetic effects (i.e. non-linear responses across developmental stages) rather than only testing differences at the end of the experiment. I measured activity on three occasions (days 1, 4, and 7). For each tub, I counted the number of tadpoles moving. I used the mean proportion of tadpoles active per tub as my behavioral response and ANOVA's to test for differences among treatments at each of the three sampling periods. All proportional data were arcsine transformed prior to analyses.

Direct Effects of Predators on Growth, Development, and Survival

I used outdoor mesocosm experiments to examine the direct impacts of predators on survivorship and development of *S. couchii* tadpoles. This experiment differs from the

laboratory experiment described above in that predators living in the mesocosms were actively preying upon tadpoles. Thus, predators were reducing tadpole densities via predation throughout the entire experiment. I used plastic pools (1.2 m in diameter and 0.3 m tall) as my experimental arena. Each pool was filled with 40 gallons of well water, 19 liters of soil, and covered with 60% shade cloth to prevent colonization by aquatic invertebrates. A total of 104 tadpoles were placed in each pool. The experimental design consisted of a control (no predators) and a predator treatment (2 hydrophilid beetle larvae). Although this environment is artificial, the conditions are very similar to those found in seasonal temporary pools in desert environments (Dayton unpublished data).

I used a completely randomized design with treatments randomly assigned to pools. Treatments were replicated 4 times each. *Scaphiopus couchii* eggs were collected from multiple clutches from 3 sites in the field and reared to hatching in the lab, at which time the tadpoles were introduced to the pools. Predators were collected from two temporary pools and introduced into the mesocosms on the same day as the tadpoles. Pools were monitored every other day for tadpoles undergoing metamorphosis and experiments were terminated after 60 days. I used t-tests to examine differences in three fitness measures: survival, time to metamorphosis, and size (Berven 1990) between controls and experimental groups.

Results

There were no significant differences in tadpole growth and development among treatments at any point during the experiment (Figs. 20-21). Nor were there significant differences between treatments in the mean proportion of tadpoles active on any given sampling period (Fig. 22). In the mesocosm experiments tadpole survivorship was significantly higher in the no-predator treatment ($t_{0.05,6}$=3.272, $P < 0.011$; Fig. 23). Time to metamorphosis was also significantly longer in the no-predator treatment ($t_{0.05,6}$=6.016, $P < 0.002$; Fig. 24). There were no significant differences in size between the two treatments ($t_{0.05,6}$=1.022, $P < 0.342$; Fig. 25).

Discussion

Although predator-induced changes in behavior and growth are widespread among aquatic organisms (Black and Dodson 1990, DeWitt et al. 2000, Relyea 2001), they are not ubiquitous. Results from my laboratory experiments show that *S. couchii* tadpoles are naïve to the presence of predators. Tadpoles do not reduce their activity rates, growth, or development when exposed to the non-lethal and lethal presence of predators. As a result *S. couchii* tadpoles are very susceptible to predation. It is this

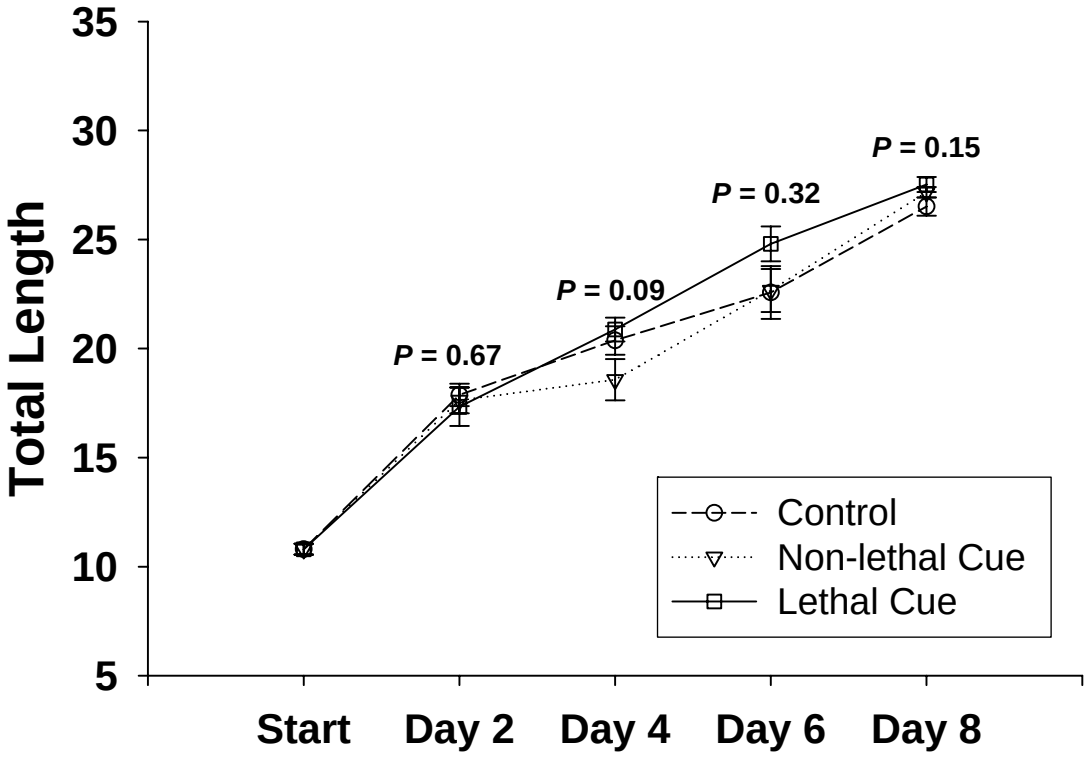

Figure 20. Size of tadpoles raised in the presence or absence of non-lethal and lethal predatory cues. *P*-values were calculated using ANOVAs on data from each sampling interval of the laboratory experiment. Error bars = ± 1 SEM.

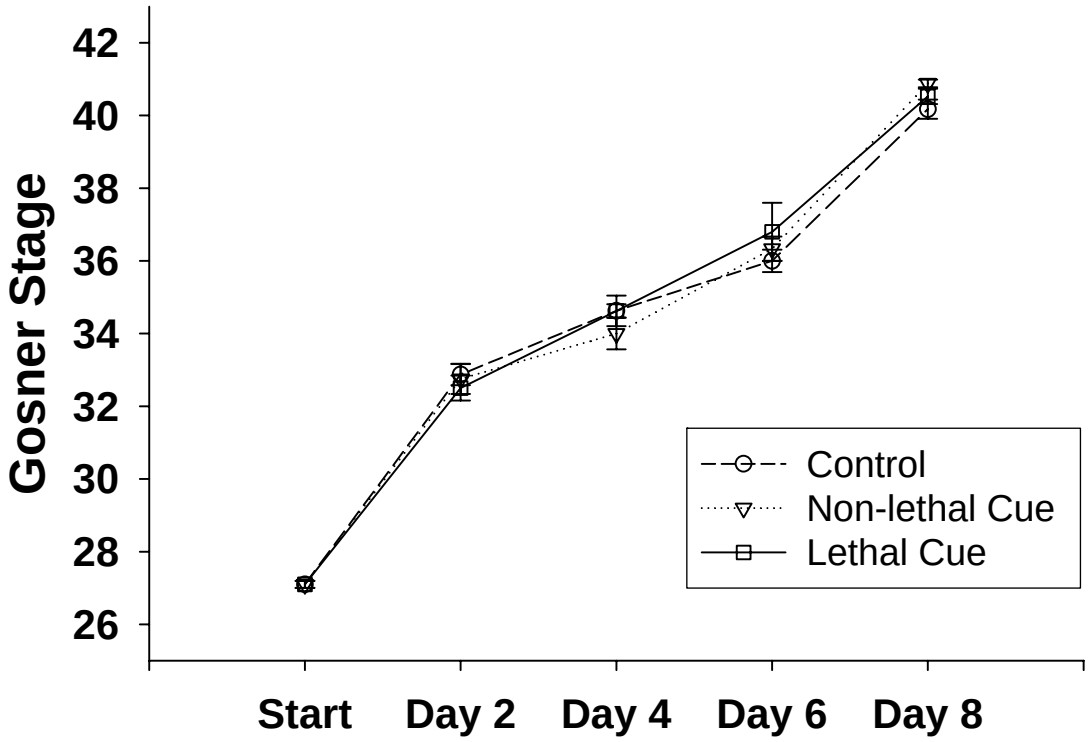

Figure 21. Developmental stage of tadpoles raised in the presence or absence of non-lethal and lethal predatory cues. *P*-values were calculated using ANOVAs on data from each sampling interval of the laboratory experiment. Error bars ± 1 SEM.

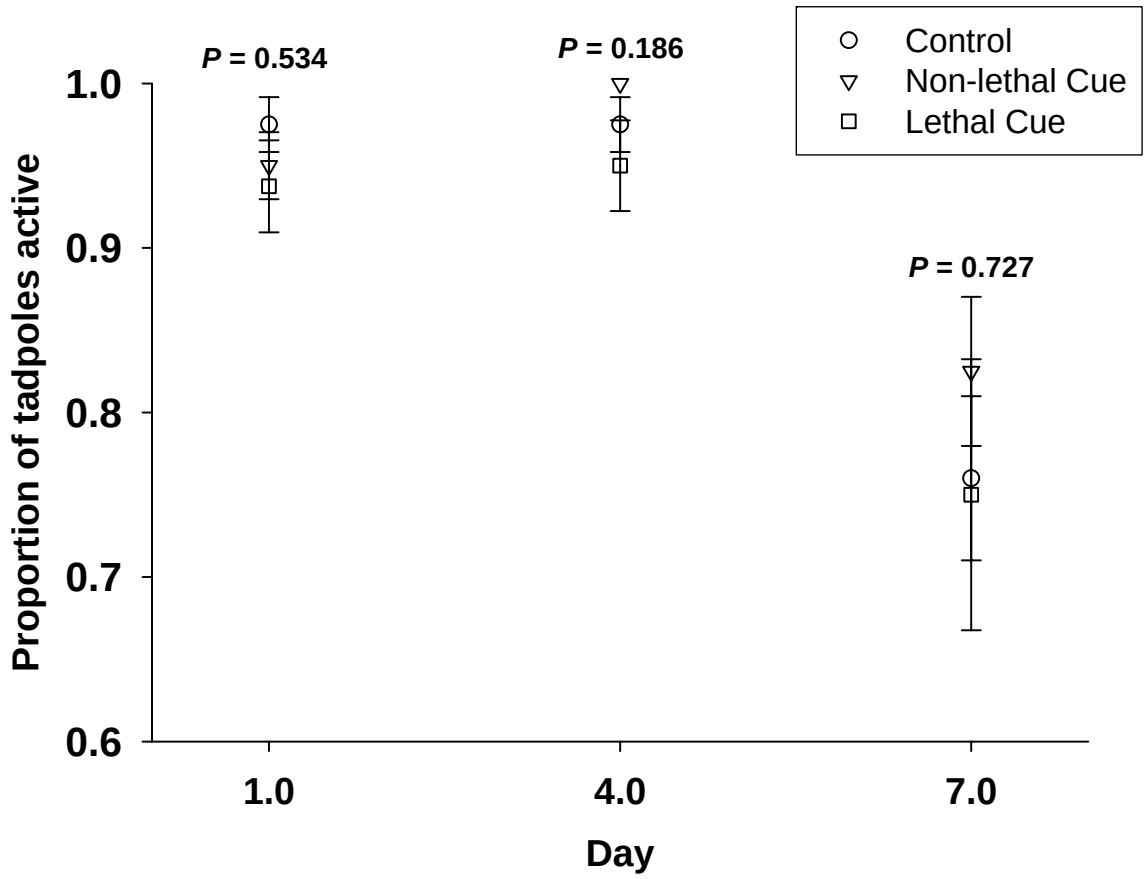

Figure 22. Proportions of tadpoles active per observation in each of the three experimental treatments. *P*-values were calculated using ANOVAs on data from each sampling interval of the laboratory experiment. Error bars ± 1 SEM.

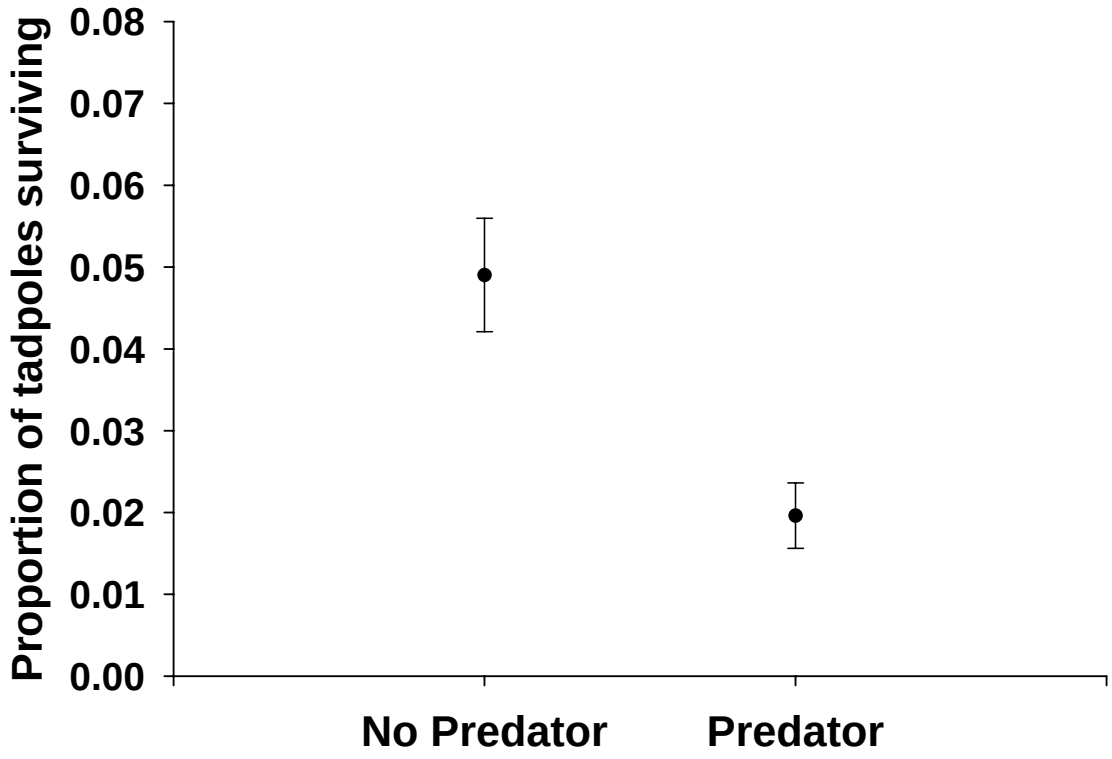

Figure 23. Mean proportion of tadpoles surviving in the control and predator treatments of the mesocosm study. Error bars ± 1 SEM.

Figure 24. Mean time to metamorphosis for the control and predator treatments of the mesocosm study. Error bars ± 1 SEM.

Figure 25. Mean size of metamorphosing individuals in the no predator and predator treatments. Error bars ± 1 SEM.

susceptibility to predators that in turn sets the stage for a reduction in time to metamorphosis for surviving tadpoles due to increased availability of per capita resources. Thus, being predator-naïve is likely to enhance cohort survival of *S. couchii* tadpoles by speeding up the time to metamorphosis in short highly ephemeral pools where desiccation is the primary cause of death.

The addition of predators into mesocosms significantly decreased survivorship of tadpoles; however, average time to metamorphosis was accelerated by over 30 days and there were no differences in sizes of metamorphosing individuals between the two treatments. The delay in time to metamorphosis exhibited in the no-predator treatment was remarkably long considering that the mean time to metamorphosis for *S. couchii* tadpoles in the field is 7-10 days (Newman 1987, Morey and Reznick 2000) and the majority of pools dry up in less than 2 weeks (Newman 1989). Based on results from my laboratory experiments, the differences in time to metamorphosis observed in the mesocosm experiments were not a result of decreased developmental rates or other predator-induced changes in growth and behavior. Rather, decreased time to metamorphosis was likely due to thinning effects of predators on tadpole densities, which resulted in an increase in per capita resources. My results are consistent with other studies that have shown a competitive release due to thinning of competitors by predators. Although there is little variation in larval periods for *S. couchii* when resources are present and abundant (Morey and Reznick 2004), time to metamorphosis can be significantly delayed or not take place at all when per capita resources are low (Newman 1987, Morey and Reznick 2000, Morey 2001). Although *S. couchii* tadpoles

have been shown to prolong development by a few days and metamorphose at larger sizes in large pools with abundant resources (Newman 1989, 1994), this was not the case in my experiments. I found no differences in size of tadpoles metamorphosing between the two treatments (i.e. tadpoles in both treatments seem to have metamorphosed as soon as they could).

The fact that predator-induced changes often occur early in ontogeny and disappear later can be problematic in interpreting experimental results (Van Buskirk and Yurewicz 1998, Relyea and Werner 2000, Laurila et al. 2004), but I measured development, growth, and behavior at multiple periods throughout the laboratory experiment. Hence, I was able to compare differences at several ontogenetic stages. Additionally, although density changed throughout the laboratory experiment, I was able to control for potential thinning effects on behavior and growth (Morey 2001, Relyea 2002b) by holding density constant across treatments. My methods were robust and I found no predator-induced changes in any of the response variables at any point during the study. Results from the mesocosm experiments showed that *S. couchii* tadpoles were very susceptible to predation; however, predators reduced densities of competitors and as a result significantly decreased time to metamorphosis for surviving tadpoles in the predator treatments.

My findings support the hypothesis that the costs of altering behavior and development (costs of phenotypic plasticity) may reduce fitness of organisms that inhabit highly ephemeral environments by reducing growth and delaying development, which in turn can be lethal in rapidly drying habitats. These types of non-lethal predator

effects are expected to be greatest for individuals inhabiting environments with little resource competition (Van Buskirk and Yurewicz 1998), high predator loads (Lardner 2000), and stable environments (Maurer and Sih 1996). Predators should have a negative effect on individuals when they lack defenses or the costs of predator avoidance outweigh the benefits (Skelly 1992). Thus, if organisms are capable of altering their behavior or developmental responses in the presence of predators, it would be expected that they would do so in environments where resources are not limited and the aquatic environment is stable. I created such an environment for *S. couchii* tadpoles in the laboratory and found no response to the presence of predators. The lack of any induced defense by *S. couchii* tadpoles was evident in the mesocosm as well as the laboratory experiments. The result that tadpoles reared in predator treatments had significantly lower survivorship than tadpoles reared in control treatments is consistent with other studies that have examined the susceptibility of organisms that inhabit ephemeral aquatic environments to predators (Woodward 1983, Walton 2001).

Although predator-induced shifts in behavior and growth are important adaptations for many organisms, the costs of reduced growth and delayed time to metamorphosis are likely too costly for species such as *S. couchii* that inhabit extremely ephemeral aquatic environments where 60-90% of all reproductive efforts fail primarily due to pond desiccation and depleted resources prior to any metamorphosis occurring (Newman 1987, 1989, Morey and Reznick 2000, Morey and Reznick 2004). The lack of predator-induced defenses makes individuals susceptible to predation and it is this susceptibility that limits ephemeral pond-breeding organisms from utilizing longer-

lasting sites where predators are more abundant (Werner et al. 1983, Woodward 1983). Although predators are not common in short-lived ephemeral pools, they are occasionally present and can eliminate entire cohorts of *S. couchii* larvae (Newman 1987).

Clearly, there is a fine line between too much predation and just the right amount. In ephemeral aquatic habitats where competition for resources can significantly reduce survivorship by delaying time to metamorphosis and increasing the probability of death by desiccation, predation may serve as an important thinning mechanism that facilitates the persistence of prey species. Indeed, on several occasions I have observed significant reductions in density of *S. couchii* tadpoles in the field as a result of predation from Hydrophilid beetle larvae and *Kinosternon flavescens* (Yellow-mud turtle) and, as a result, have noticed significant increases in the size and number of surviving tadpoles. My observations mirror those of other studies (Newman 1987) in which Hydrophilidae and other predators significantly reduced, or completely eliminated, *S. couchii* tadpoles in natural pools. The positive effects of predation on surviving *S. couchii* tadpoles may be especially important during drought years when seasonal rains are less frequent and pool duration is even shorter compared to years when rainfall is abundant. Alternatively, in years when water is plentiful and pools long-lasting, predation pressure may completely eliminate cohorts of tadpoles from late-arriving adults trying to breed in long-lived pools where predator densities are high.

Being predator-weary can reduce cohort success

I conducted mesocosm experiments on three other species, *Gastrophryne olivacea*, *Bufo debilis*, and *Bufo punctatus,* to examine the influence of predators on survival and time to metamorphosis. These experiments, and the statistical analyses, followed the same methods used in the mesocosm experiment described above and were conducted at the same time period. My results indicate that predators reduce survivorship and speed up time to metamorphosis for *B. punctatus*, however, *G. olivacea* and *B. debilis* showed no difference in survivorship or time to metamorphosis (Figs. 26-27). I suggest that *B. punctatus* is predator-naïve and that predators may enhance cohort survivorship via thinning effects, as I have suggested for *S. couchii*. The lack of any significant differences in survivorship between control and predator treatments for *G. olivacea* and *B. debilis* suggests that these two species are better adapted for escaping predators. Being predator-weary has clear advantages in environments where predator loads are high. Such environments are common in long-lived ephemeral pools in Big Bend National Park (Dayton unpublished data). My results suggest that *B. debilis* and *G. olivacea* evade predators and, as a result, tadpole densities remain relatively high even when predators are present. As a result per capita resources are low and time to metamorphosis is delayed. Thus, in the case of *B. debilis* and *G. olivacea,* being predator-weary may actually decrease cohort success in short-lived, resource-poor sites due to a delay in time to metamorphosis (which increases the probability of death by desiccation) as a result of high levels of intraspecific competition.

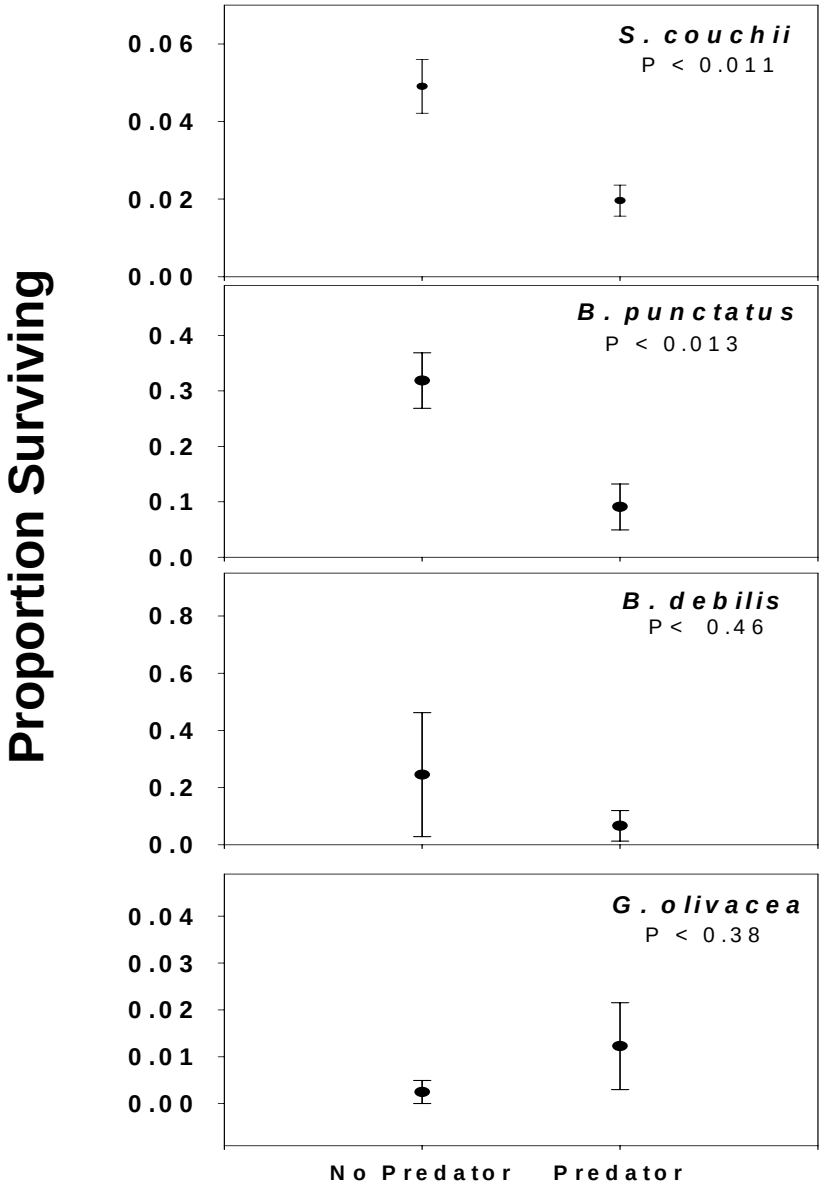

Figure 26. Mean proportion of tadpoles surviving in the control and predator treatments of the mesocosm study. *S. couchii* included for comparison. Error bars ± 1 SEM.

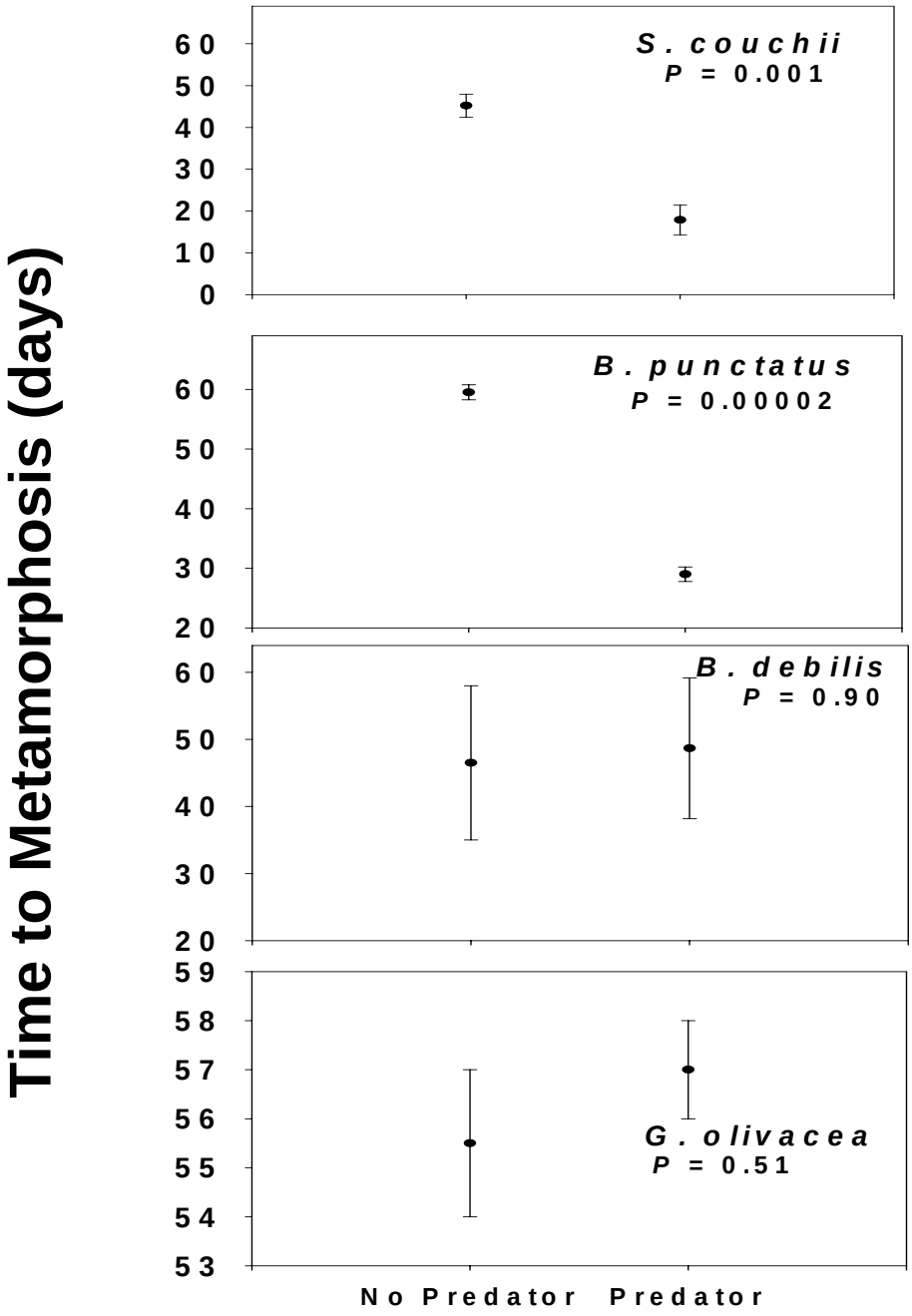

Figure 27. Mean time to metamorphosis for the control and predator treatments of the mesocosm study. *S. couchii* included for comparison. Error bars ± 1 SEM.

Summary

The lack of predator-induced defenses in *S. couchii* is not surprising considering its life history and the stochastic and harsh environment in which it lives. However, it is difficult to tease apart whether the lack of predator-induced defenses is a result of the environment, phylogeny, or both. Although predator-induced defenses are wide-spread among a diverse group of species, the two other studies that have examined predator-induced changes in behavior and growth in Pelobatid frogs (*Pelobates fuscus* and *P. cultripes*) found no predator-induced changes when tadpoles were exposed to predatory beetle larvae (Tejedo 1993, Lardner 2000). These studies combined with my results suggest that the inability to respond to the presence of predators may at least partially reflect historical constraints within the family Pelobatidae rather than habitat duration alone. Recent studies examining phylogenetic inertia and habitat duration on prey defenses and development suggest that both phylogeny and habitat duration are important in influencing predator-induced defenses and developmental rates (Maurer and Sih 1996, Sih et al. 2000, Suhling et al. 2005). Future studies examining behavioral and morphological impacts of predators on closely related species that inhabit opposite ends of the hydroperiod gradient, as well as studies examining diverse lineages of organisms that inhabit highly ephemeral aquatic environments, will provide important insight into the roles that phylogeny and environment play in influencing predator defenses.

CHAPTER VI

MICROHABITAT SEGREGATION AMONG DESERT ANURANS

Overview

Very little is known about the factors that structure desert anuran communities. The purpose of this study was to examine microhabitat segregation of the aquatic environment among four desert anurans: *Scaphiopus couchii* (Couch's Spadefoot), *Bufo debilis* (Western Green Toad), *Bufo punctatus* (Red-spotted Toad), and *Gastrophryne olivacea* (Narrow-mouthed Toad). I surveyed the occurrence of species at breeding sites, and examined variation in microhabitat characteristics among breeding sites. I also conducted reciprocal transplant experiments of tadpoles in mesh enclosures to test the species performance in different habitats in the absence biotic factors. The four species exhibit non-random patterns of co-occurrence at breeding sites across the Chihuahuan Desert landscape. The canonical axes derived from the discriminant analysis revealed the species differed in breeding habitat characteristics along an environmental gradient dominated by substrate and bank cover. At one end of the gradient *B. punctatus* was associated with sites characterized by rocky substrate and low bank cover, at the other end of the axis *B. debilis* was associated with sites that had clay and silt substrata and high bank cover. *Scaphiopus couchii* and *G. olivacea* exhibited intermediate scores but were more similar to *B. debilis* than to *B. punctatus*. Reciprocal transplant experiments of larval anurans among sites where they naturally occurred and sites where they were not known to occur revealed no significant differences in

survivorship for any of the species. Taken together, my results suggest that although abiotic components of the breeding site differed among some species, it is very unlikely that breeding site characteristics play a large role in the non-random patterns of occurrence of these species across the landscape.

Introduction

The field of community ecology has benefited greatly from studies examining the factors that regulate the distribution and abundance of anurans (Morin 1983, Wilbur 1997, Skelly et al. 1999). However, the majority of what we have learned pertaining to the mechanisms that structure amphibian communities comes from studies conducted in eastern United States (Wilbur 1982, Morin 1986, Werner 1992) and tropical forests of Central and South America (Heyer et al. 1975, Gascon 1991, 1995). High rainfall over large areas in these regions creates a heterogeneous environment of pools that generally persist for several months, allowing amphibians with a large range of larval developmental periods to successfully reproduce. Characteristics of temperate and tropical environments provide a relatively stable and predictable habitat that supports greater amphibian species richness compared to desert regions (Sullivan 1989). Moist conditions and extensive forest cover in these regions provide suitable habitat for movement of adults between pools, and the extended hydroperiod enables a succession of asynchronous breeding of species at any given pond throughout the year (Oseen and Wassersug 2002). Breeding sites with long hydroperiods also tend to harbor aquatic and terrestrial predators that are known to play an important role in structuring amphibian

communities in these regions (Wellborn et al. 1996). In contrast, deserts are characterized by patchy vegetation, higher temperatures, and highly variable, seasonal, precipitation that varies in location, intensity, and frequency on a year to year basis (Whitford 2002). Amphibians in desert ecosystems usually breed in a given pool only once a year and often do not breed on an annual basis due to unpredictability of seasonal rains (Bragg 1961, Woodward 1984). Characteristics of temperate and tropical environments provide a relatively stable and predictable habitat that supports greater amphibian species richness compared to desert regions.

Although we have a thorough understanding of many of the factors that influence the persistence of anurans in temperate and tropical regions, very little is known about the factors that are important in structuring the species composition of desert anuran communities (Woodward and Mitchell 1991). There have been only a few studies that have examined interspecific interactions in desert anuran communities (Woodward 1982a, 1982b, 1983, Woodward and Johnson 1985), and all but one of these focused on interactions among species that inhabit either ephemeral or permanent sites. Results from these studies suggest that the distribution of anurans in desert environments is largely determined by a competition-predation trade-off between tadpoles of species that inhabit short-lived versus long-lived aquatic sites. Species that breed in ephemeral sites tend to be superior resource competitors when reared with species that breed in permanent sites; however, they are also more susceptible to predators which are more abundant in permanent sites. These studies were influential in helping to understand the biotic factors that resulted in the segregation of temporary and permanent pond-breeding

anurans; however, they did not elucidate factors that structure assemblages of anuran species that breed only in ephemeral desert pools.

Recent work has shown that although desert-dwelling anuran species are sympatric at the regional scale, they exhibit non-random patterns of co-occurrence at both the landscape level and at specific breeding sites (Dayton and Fitzgerald 2001, Dayton et al. 2004). At the landscape level, species tend to be associated with specific soil types and, although some species tend to occur in a broader array of habitat types than others, there is substantial overlap among species distributions at this spatial scale (Dayton et al. 2004). At the scale of individual breeding sites, species co-occur in non-random patterns, co-occurring less frequently then expected (Dayton and Fitzgerald 2001). Similar to the mechanisms shaping temperate and tropical anuran assemblages, competitive abilities and susceptibility to predation among tadpoles in ephemeral desert pools seem to play an important role in determining species composition at individual breeding sites for some but not all species (Dayton and Fitzgerald 2001). While these studies have begun to elucidate the importance that biotic interactions and landscape-level habitat associations have on the distribution of desert anurans, the role that abiotic factors of the breeding site have on species composition is largely unknown (Woodward and Mitchell 1991).

As part of my research examining the ecology of desert anurans, I conducted studies to determine the role that the characteristics of the breeding site have on influencing the distribution of four desert-dwelling anurans: *Scaphiopus couchii* (Couch's Spadefoot Toad), *Bufo punctatus* (Red-spotted Toad), *Bufo debilis* (Western

Green Toad), *and Gastrophryne olivacea* (Plains Narrow-mouthed Toad). Specifically, I conducted surveys for the presence and absence of these four species in ephemeral pools in Big Bend National Park, Texas, and measured and compared microhabitat data among species. I also conducted reciprocal transplant experiments of tadpoles among sites where species are known to breed and sites where they do not occur, to examine the influence of water quality on survival of tadpoles in the absence of the direct effects of competition and predation.

Methods

Breeding Habitat Surveys

During the summer months of May - August from 2002 to 2004 I conducted area-constrained surveys (patch sampling) (Jaeger 1994) at temporary water bodies throughout all of Big Bend National Park for the presence of amphibians. Surveys were conducted over a 3-year period, and covered the range of available habitats throughout the entire study region. To document species I used extensive dip-net sampling for tadpole presence. Dip-net surveys provide a good estimate of species presence (Shaffer et al. 1994) and are effective in detecting tadpoles even when densities are relatively low (Jung et al. 2002b). Tadpoles were collected in the field and later identified to species. I used the program Ecosim to test the null hypothesis that the observed pattern of species co-occurrence at breeding sites was non-random. Ecosim allows you to test for non-random patterns of species co-occurrence using a presence-absence matrix. I used Stone and Robert's (1990) co-occurrence index (C-score) and the default randomization

algorithm that maintains fixed sums for rows and columns; for more information see Stone and Roberts (1990) and Gotelli (2000).

Habitat characteristics of the breeding site were assessed by measuring width, length, depth, and substrate. Width was measured by taking 3 bank-to-bank measurements equally spaced across the short axis of the pool and calculating the mean width. Length was determined by measuring the distance from bank-to-bank along the longest axis of the pool. Depth was recorded by taking 9 depth measurements at equal distances along the width measurements. Substrate was recorded by hand sampling substrate at the same localities as the depth measurements and categorized as follows: Boulder/Bedrock (>250 mm) = 6, Cobble (50-250 mm) = 5, Pebble (15-50 mm) = 4, Gravel (2-15 mm) = 3, Sand (~.06-2 mm) = 2, silt and clay (< 0.06 mm) = 1. Percent bank cover, canopy cover, and emergent vegetation was recorded by visually estimating the percent coverages.

All percentage data were converted to proportions and arcsine transformed, and linear measurements were log transformed, to meet assumptions of normality prior to all statistical analyses. I performed a discriminant analysis to determine the accuracy with which I could assign individuals to the proper species based on the linear combination of habitat variables. I then conducted an Analysis of Variance (ANOVA) on the first canonical score derived from the discriminant analysis followed by Tukey's post hoc test to test for differences among species. In pools where I found more than one species, data were replicated so that there was always only one species per sample. For example, if at a given site *S. couchii* and *G. olivacea* co-occurred, the data were replicated for

each species and input as two separate sites. Thus, my results include environmental data for each species at every site it was found.

Reciprocal Transplant Experiments

During the summer months of 2003-2004, I conducted reciprocal transplant experiments of *S. couchii, B. punctatus, G. olivacea,* and *B. debilis* tadpoles in ephemeral pools in Big Bend National Park. Tadpoles between Gosner stages 25-30 (Gosner 1960) were collected from the field and placed in control and experimental mesh enclosures (45 x 30 x 30 cm; 2-mm mesh). The use of enclosures exposes tadpoles to conditions of the abiotic environment (i.e. DO levels, pH, conductivity, temperature, etc.), while excluding direct effects of predators and competitors (Berven 1990, Gascon 1995). Ten conspecific tadpoles were placed in each enclosure at each site. My design consisted of a control (caged tadpoles in naturally occurring site) and a treatment (caged tadpoles translocated to a site where they do not naturally occur). Tadpoles were in transit no longer than 45 minutes between any two sites. Pilot studies examining the effect of translocation of tadpoles among sites indicated that translocation did not influence survivorship (Dayton personal observation). Experiments were replicated 7-10 times for each species, however, flash floods, desiccation, and predation by turtles eating through enclosure walls resulted in the termination of several of the experiments. As a result, replicates were as follows: *S. couchii* = 6, *B. punctatus* = 5, *B. debilis* = 4, *G. olivacea* = 4. Site location was based on presence absence data of each species collected

over the past 6 years. I used a t-test to examine differences in survivorship between control and experimental treatments.

Results

Co-occurrence Patterns

I detected tadpoles in 87 temporary pools. Of those pools, 68 had one species, 13 had two species, 6 had three species, and none had 4 species. *Bufo punctatus* was found primarily by itself; *Scaphiopus couchii* occurred primarily by itself or with *G. olivacea* or *B. debilis*; *Gastrophryne olivacea* was found primarily with either *S. couchii* or *B. debilis* but not *B. punctatus*; *B. debilis* was found primarily with *S. couchii* and *G. olivacea* (Table 5). The observed C-score data from my Ecosim analysis was significantly greater ($P < 0.00001$) than the simulated data (C-scores observed = 423.33; simulated = 338.21), suggesting that species tend to co-occur less frequently than expected if they inhabited breeding pools in a random manner.

Microhabitat Variation

Results from the discriminant analysis using environmental variables to classify individuals into species groups were varied; 29% of *G. olivacea*, 22% of *S. couchii*, 46% of *B. debilis*, and 95% of *B. punctatus* were correctly classified to species (Table 6). The first canonical variate axis explained 92% of the cumulative variance (Table 7). High loadings on the first canonical axis represented sites with small substrate size, little vegetation structure in the water, and abundant bank cover (Fig. 28). ANOVA

Table 5. Number of times each species was detected by itself and with other species.

Species	*n*	*S. couchii*	*B. punctatus*	*G. olivacea*	*B. debilis*
S. couchii	27	10	5	8	9
B. punctatus	60		53	2	1
G. olivacea	12			3	5
B. debilis	13				2

Table 6. Number and percentage of times each of the four species was correctly classified by discriminant analysis using recorded microhabitat variables.

	Predicted classification				
Observed classification	*G. olivacea*	*S. couchii*	*B. debilis*	*B. punctatus*	Correctly classified
G. olivacea	4	2	2	6	29%
S. couchii	3	6	7	11	22%
B. debilis	3	4	6	0	46%
B. punctatus	0	2	1	56	95%

Table 7. Standardized coefficients variables for the first three canonical axes of the discriminant analysis.

Microhabitat variables	Axis 1	Axis 2	Axis 3
% Canopy	-0.029428	0.370636	0.609715
% Vegetation in Water	-0.209792	0.311298	-0.581664
% Bank Cover	0.555442	0.439425	0.174314
Length	0.140971	-0.181683	0.223152
Mean Width	-0.010792	0.539156	-0.365782
Mean Substrate Size	-0.647923	0.587840	0.099188
Mean Depth	0.028629	0.008967	0.464364
Eigenvalue	1.003730	0.075864	0.009127
Cumulative % Var. Explained	0.921935	0.991617	1.000000

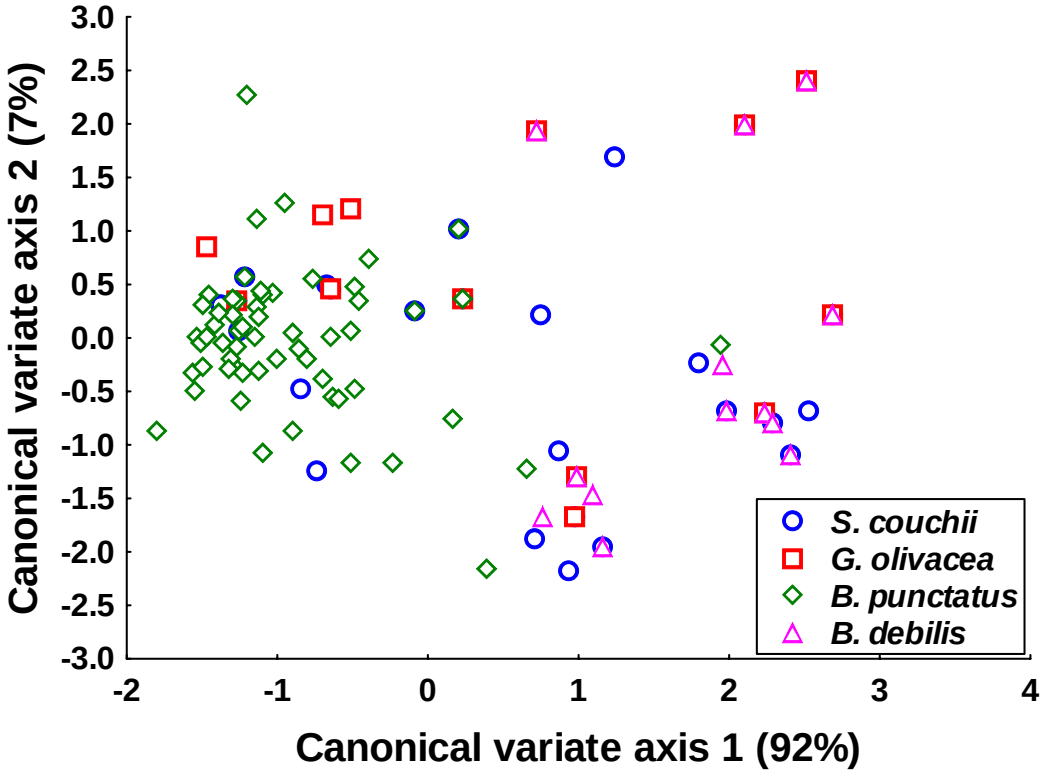

Figure 28. Position of all breeding sites in discriminant space obtained by canonical variate analysis on microhabitat variables.

revealed significant differences among species scores on the first canonical axis ($F_{3,109}$ = 36.469, $P < 0.00001$; Fig. 29). Tukey's post hoc tests showed that *Bufo punctatus* had significantly lower canonical axis scores than all other species ($P < 0.001$), *S. couchii* scored significantly lower than *B. debilis* ($P < 0.014$) but not *G. olivacea* ($P = 0.99$), and *G. olivacea* scored significantly lower than *B. debilis* ($P = 0.045$).

Reciprocal Transplant Experiments

There were no significant differences in survival between control and experimental groups for any of the species (*S. couchii* = $t_{0.05,10} = 0.600$, $P = 0.562$; *B. punctatus* = $t_{0.05,10} = 1.195$, $P = 0.272$); *B. debilis* = $t_{0.05,6} = 0.513$, $P = 0.562$; *G. olivacea* = $t_{0.05,6} = 1.806$, $P = 0.147$).

Discussion

The objective of my study was to examine variation in breeding habitat characteristics among four desert-adapted anurans and to determine whether abiotic components of the breeding habitat influenced survivorship in the absence of direct effects of competition and predation. Results from my breeding site surveys indicated that although *S. couchii*, *B. debilis*, *G. olivacea*, and *B. punctatus* often breed within short distances of one another, they exhibit a non-random pattern of co-occurrence at individual breeding sites. These results support previous findings that found similar patterns of co-occurrence for these and other desert anuran species (Dayton and Fitzgerald 2001). Comparisons of microhabitat characteristics at breeding sites showed

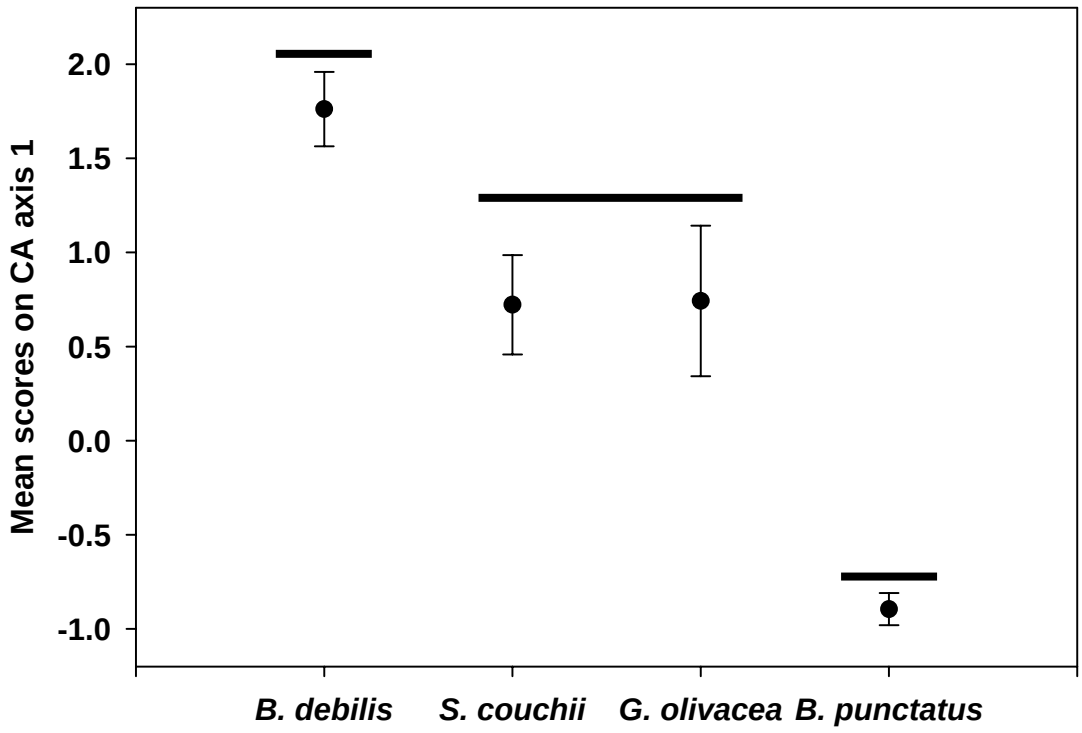

Figure 29. Mean scores of the first canonical variate axis. Bars above symbols represent homogenous subsets as determined by Tukey's post hoc tests (significant at $P < 0.05$). Error bars ± 1 SEM.

that species segregate among sites along an environmental gradient dominated by substrate size and bank cover. *Bufo punctatus* and *B. debilis* exhibited the most extreme differences in habitat affinities, with *B. punctatus* associated with rocky sites that had relatively little bank cover, and *B. debilis* associated with sites that had fine substrata and dense bank cover. *Scaphiopus couchii* and *G. olivacea* were associated with intermediate sites, though they tended to occur in sites that were similar to those of *B. debilis*. Discriminant analysis correctly classified 95% of all *B. punctatus* based on microhabitat scores, however, correct classification for each of the remaining species was less than 50%. Results from my reciprocal transplant experiments revealed no differences in survivorship of tadpoles reared in either natural or unnatural sites in the absence of direct biotic factors, suggesting that abiotic components of the aquatic environment do not limit the distribution of these species.

Breeding site characteristics have important fitness consequences for anurans with free-swimming larvae. If tadpoles do not successfully complete metamorphosis, the fitness of the individual is zero. As a result, many anurans seem to select breeding sites based on the abiotic and biotic components of the pond (Petranka et al. 1994, Spieler and Linsenmair 1997, Matsushima and Kawata 2005). In my study, although microhabitat characteristics of the breeding site did vary among some species, results suggest that microhabitat of breeding sites, and the aquatic environment in the absence of biotic factors, do not play large roles in influencing the distribution of *S. couchii*, *G. olivacea*, *B. debilis*, and *B. punctatus*. Several phenomena have been suggested to lead to habitat segregation among pond-breeding anurans in temperate and tropical regions,

including resource competition (Wilbur 1982, Kupferberg 1997, Smith et al. 2004), predation (Heyer et al. 1975, Morin 1983, Magnusson and Hero 1991), and physiological constraints (Glos et al. 2003), and hydro period (Wellborn et al. 1996, Semlitsch 2000, Eason and Fauth 2001). All of these factors are centered on survival of tadpoles. In temperate and tropical environments where the terrestrial environment is relatively stable, refugia for adult anurans may not be a limiting factor. However, in xeric regions where fluctuations in the environment are extreme and the hot, dry conditions are lethal for exposed adult anurans, variation in natural history strategies of adult anurans may play a critical role in influencing the persistence of species across the landscape. Indeed, in my previous studies I have shown that the distribution of desert anurans at the landscape level are non-random and tend to be significantly influenced by soil type (Dayton et al. 2004). At the landscape level, adult *S. couchii* and *B. debilis* tend to be associated with fine soils that are high in clay content, whereas *B. punctatus* are associated with rocky soils (Dayton et al. 2004). *Gastrophryne olivacea* are associated with a wide range of soil types, ranging from silt-clay loams to coarse rocky soils (Dayton unpublished data). Thus, the variation in microhabitat at the breeding sites that I observed may largely reflect the landscape-level habitat associations of these species, which are likely a result of constraints upon the adult life stage (e.g. refugia for adults during dry periods). However, in the current study as well as a previous study (Dayton and Fitzgerald 2001), I found that species tend to segregate among breeding sites even when they are in close proximity to one another, suggesting that factors at the breeding site level are also important in influencing breeding site use.

The fact that I found no significant differences in survival of tadpoles between natural and transplanted sites suggests that biotic rather than abiotic factors may play an important role in structuring the species composition at the level of the breeding site. Previous studies have shown that desert anuran tadpoles vary in competitive abilities and susceptibility to predation (Woodward 1982a, Newman 1987, Dayton and Fitzgerald 2001). Although predator abundance and richness is low in ephemeral pools compared to intermediate and permanent pools (Spencer et al. 1999, Babbitt et al. 2003, Peltzer and Lajmanovich 2004), the few studies that have examined the effects of predators on desert-larval anurans that breed in ephemeral pools suggest that they may play an important role in shaping distribution patterns of anurans in xeric environments (Dayton and Fitzgerald 2001). When teasing apart factors that limit species distributions it is difficult, if not impossible, to separate out all the potential affects. Although factors influencing community composition of temperate and tropical anuran assemblages are thought to be more complex than those influencing desert anuran species assemblages (Woodward and Mitchell 1991), results from this study combined with recent research suggest that mechanisms responsible for shaping desert anuran communities are in fact complex and are influenced by a combination of factors, ranging from the landscape scale down to variation in abiotic and biotic components of the breeding site.

CHAPTER VII

CONCLUSIONS

Previous research on amphibian communities in temperate and tropical regions supports the hypothesis that a balance between permanency of water, length of tadpole stage, competitive ability of tadpoles, and presence of predators may largely determine how many species of amphibians are distributed across the landscape. However, these mechanisms had not been tested for desert anurans that breed in highly ephemeral sites. The goal of my dissertation was to examine how abiotic and biotic factors at multiple spatial scales influence the distributions of a guild of ephemeral pool-breeding amphibians: *Scaphiopus couchii*, *Bufo debilis*, *Bufo punctatus*, and *Gastrophryne olivacea*. My results emphasize the fact that it is important to consider factors that influence the persistence of both the adult and larval stage. At the landscape level, species were differentially associated with specific environmental variables. Predicted suitable habitat for *S. couchii* and *B. debilis* is relatively sparse compared with that of *B. punctatus* and *G. olivacea*. This difference is most likely due to species-specific life history traits of the adult life stage. *Scaphiopus couchii* and *B. debilis* are more habitat specialists than *B. punctatus* and *G. olivacea*. High-quality habitat for *B. debilis* and *S. couchii* is primarily confined to flat regions with fine loam soils. These species are both known to take refuge by burrowing into the soil. In comparison, High-quality habitat for *B. punctatus* and *G. olivacea* is relatively widespread throughout the park. Compared

with *S. couchii* and *B. debilis*, these two species can be considered habitat generalists, with adults taking refuge during dry periods in a wide variety of places.

Although species differed in their distribution patterns throughout Big Bend National Park in localities where all four species co-occur, there is segregation among species within individual breeding pools; very rarely do more than two species co-occur in the same pool. Results from my reciprocal transplant studies indicate that when controlling for potential direct effects of predation and competition, abiotic components of the aquatic environment do not constrain species from inhabiting pools where they do not naturally occur. At the scale of the breeding site, although microhabitat characteristics vary significantly among some species, there is a lot of overlap in habitat characteristics.

Laboratory and mesocosm experiments examining indirect and direct effects of predators on survival, growth, and time to metamorphose for the most xeric-adapted species, *S. couchii*, suggest that predation may play an important role in influencing the distribution of this species. *Scaphiopus couchii* tadpoles did not alter their behavior, growth, or development in response to lethal and non-lethal cues emitted by predators and tadpoles that were consumed. These results combined with my mesocosm experiments, previously published data (Newman 1987, Dayton and Fitzgerald 2001), and field observations that have shown *S. couchii* tadpoles to be very susceptible to predators and in some cases completely eliminated from temporary pools as a result of predation, suggest *S. couchii* tadpoles do not exhibit fixed or plastic defense mechanisms that commonly occur in numerous other aquatic organisms (Relyea and Werner 1999,

Van Buskirk and McCollum 1999, DeWitt et al. 2000, Lardner 2000, Langerhans and DeWitt 2002, Relyea 2003, 2004). The lack of induced defenses leaves *S. couchii* tadpoles extremely susceptible to aquatic predators and, as a result, excludes them from using pools with intermediate or long hydroperiods. Results from my mesocosm study show that, although predators significantly decrease survival rates of *S. couchii* tadpoles, they may actually be beneficial for the persistence of a cohort at a breeding site. Tadpoles reared with predators metamorphosed on average 30 days sooner than tadpoles reared in the absence of predators. These findings suggest that predation plays an important role in facilitating metamorphosis of *S. couchii* tadpoles via reduced densities and increased per capita resources for surviving individuals.

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VITA

Gage Hart Dayton was born on 26 February 1972 in San Diego, California. While growing up in Southern California Gage traveled with his family throughout the southwestern United States and Baja California. Gage graduated from Torrey Pines High School in 1990, then attended Humboldt State University in Northern California from 1990-1996. Between starting and finishing his undergraduate work Gage spent a winter at Potsdam State University in upstate New York (where he got to experience a real winter), a summer working on the Colorado River assisting in studies examining the influence of flow regulation on plant communities, and a month as a research diver in Antarctica. After graduating from Humboldt State University where he obtained his B.S., Gage worked and traveled for 2 years before he enrolled at Texas A&M University in 1999. Gage obtained his M.S. in 2001 and later his Ph.D. in 2005 from the Department of Wildlife and Fisheries Sciences. During his time at Texas A&M, Gage married Elizabeth Ryder and sired two wonderful children, Savanna and Camille. Gage's permanent address is yet to be determined, but it will be somewhere in the southwestern or western United States; in the mean time, he can be contacted at The Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258.